UNIVERSITÉ DU QUÉBEC À MONTRÉAL

QUELLES CONTRAINTES STRUCTURENT LES COMMUNAUTÉS DE POISSONS?

INFLUENCE DE L'ENVIRONNEMENT, DE LA STRUCTURE SPATIALE MULTI-ECHELLES ET DES TRAITS FONCTIONNELS SUR L'ASSEMBLAGE DES COMMUNAUTÉS DE POISSONS EN RIVIERE

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PAR
CAROLINE SENAY

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AVANT-PROPOS

Ce mémoire a été rédigé sous forme d'articles pour une future publication dans un journal scientifique international. Le premier auteur est Caroline Senay, qui a élaboré en grande partie le projet, effectué la revue de la littérature, l'échantillonnage sur le terrain, les analyses statistiques, la rédaction et la mise en page. Les co-auteurs sont Pedro Peres Neto, Ph. D., directeur du projet, et Daniel Boisclair, Ph. D., co-directeur. Ils ont encadré ce projet à toutes les étapes, de l'élaboration des questions pertinentes à la programmation de tests statistiques afin de vérifier les hypothèses. Les articles n'ont pas encore été soumis et, dans le cadre de ce mémoire, une version allongée est présentée avec des introductions et des descriptions méthodologiques plus étoffées. Les deux chapitres seront retravaillés par l'ensemble des auteurs avant soumission pour la publication.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

Tableau Page

Tableau Page

Tableau Page

RÉSUMÉ

Cette étude a été réalisée afin d'évaluer les relations entre les conditions environnementales, la structure spatiale multi-échelles et les traits fonctionnels pouvant influencer la structure des communautés. Dans le premier chapitre, l'influence à différentes échelles de l'environnement et de la structure spatiale sur divers descripteurs biologiques décrivant la distribution de 17 espèces de poissons des rivières a été déterminée. Dans le second chapitre, la relation entre l'environnement et la variabilité phénotypique de la morphologie et de la capacité de nage de 10 espèces de poissons des rivières a été évaluée.

Pour ce faire, nous avons étudié les communautés de poissons des rivières dans la région des Laurentides au Québec, Canada. Le plan d'échantillonnage représentait le réseau hydrographique de la région et était de nature hiérarchique. Il comprenait trois bassins versants (*e.g.,* rivière Rouge, du Nord et Ouareau), à l'intérieur desquels 39 sites ont été répartis et divisés en 143 sections au total, chacune associée à un type de mésohabitat (*e.g.,* rapide, droit et fosse). Pour chaque section, les poissons ont été capturés à la pêcheuse électrique, anesthésiés et photographiés afin de déterminer leur présence-absence et évaluer leurs caractéristiques morphologiques en utilisant la géomorphométrie. Également pour chaque section, des conditions environnementales ont été évaluées afin de caractériser le milieu. De plus, certains poissons ont été soumis à un protocole de nage standard au laboratoire pour déterminer leur capacité de nage soutenue.

Les résultats du premier chapitre ont souligné l'importance de l'échelle choisie en ce qui concerne la variabilité des conditions environnementales et de la distribution des poissons, en plus des patrons de cooccurrence et de diversité. Sur les 17 espèces retenues pour cette partie, 60% a sélectionné un type d'habitat particulier. La distance par voie d'eau totale entre les sites est celle qui a modélisé le plus fidèlement la structure spatiale de l'environnement et la distribution des espèces. L'environnement et la structure spatiale ont expliqué significativement les patrons de distribution et de cooccurrence. De plus, notre perception des patrons de diversité est affectée par le choix d'une approche hiérarchique ou non-hiérarchique. Le second chapitre a identifié des patrons de différentiation morphologique entre les types d'habitat pour 80% des espèces. Ces variations morphologiques sont présentes entre les populations provenant de différents mésohabitats indépendamment des bassins versants, mais ne sont pas constantes entre les espèces. Il est possible que différentes espèces aient des stratégies particulières pour surmonter des défis semblables. Les espèces qui n'ont pas démontré de divergences sont benthiques, ce qui peut expliquer qu'ils ressentent et répondent moins aux caractéristiques environnementales. Le mésohabitat ne semble pas affecter le niveau d'intégration phénotypique des populations, bien qu'il semble y avoir des différences entre les espèces. Aucune relation significative n'a été observée entre la capacité de nage et le type d'habitat, l'identité des espèces, les descripteurs reflétant la distribution ou

la sélection d'habitat et la morphologie. La mesure de capacité de nage utilisée ne semble pas représenter adéquatement les défis écologiques et physiologiques auxquels font face les poissons des rivières.

Mots clés: capacité de nage, cooccurrence, distribution, diversité, environnement, multi-échelles, multi-espèces, poisson, polymorphisme, rivière, structure spatiale.

INTRODUCTION

1.1 Problématique de l'étude et état des connaissances

Les processus qui génèrent et maintiennent l'assemblage des espèces en communautés sont des thèmes centraux et récurrents en écologie. Bien qu'étudiés depuis plusieurs décennies, certains aspects des mécanismes déterminant l'organisation naturelle des communautés demeurent incompris. Une manière conceptuelle d'aborder cette problématique est de considérer qu'il existe une diversité élevée d'espèce à grande échelle qui peut être influencée par de nombreux facteurs limitant les espèces retrouvées à petite échelle au niveau de la communauté. Ces facteurs sont d'origines diverses et peuvent affecter la structure des communautés à différentes échelles spatiales. Par exemple, les conditions environnementales peuvent déterminer si un habitat est approprié pour un organisme. Les traits fonctionnels (*i.e.*, caractéristiques décrivant la morphologie, la physiologie, l'histoire de vie ou le comportement des organismes) peuvent indiquer si les organismes sont adaptés aux conditions environnementales. De plus, les processus spatiaux, tels la dispersion et l'isolation, peuvent être responsables de l'absence de certains organismes dans une partie du territoire. Les interactions biotiques entre les individus, comme la compétition, la prédation ou la facilitation (*i.e.*, processus par lequel une espèce profite de la présence d'une autre), peuvent également limiter l'espace occupé par les organismes. Bien qu'ils soient connus, l'influence relative de ces différents facteurs sur la distribution des organismes et l'échelle à laquelle ils structurent les communautés restent à clarifier. Dans ce travail divisé en deux chapitres, plusieurs de ces facteurs seront abordés. Cette étude a été réalisée afin d'évaluer les relations entre les conditions environnementales, la structure spatiale multi-échelles et les traits fonctionnels pouvant influencer la structure des communautés de poissons en rivière. Dans le premier chapitre, l'influence de l'environnement sur divers descripteurs biologiques décrivant la distribution de 17 espèces de poissons de rivières à trois échelles spatiales sera déterminée. Dans le second chapitre, la relation entre l'environnement et la variabilité phénotypique de la morphologie et de la capacité de nage de 10 espèces de poissons des rivières sera évaluée. Finalement, une conclusion globale présentera le lien entre les deux

chapitres et leurs contributions scientifiques. En premier lieu, cette introduction sous la forme d'une revue de littérature établira le cadre général dans lequel s'inscrivent les questions abordées dans les deux chapitres subséquents. Plus précisément, les caractéristiques des réseaux hydrographiques, la problématique des échelles, les descripteurs biologiques, la variabilité phénotypique de la morphologie et la capacité de nage ainsi que l'écologie des espèces seront décrits.

Les réseaux hydrographiques ont plusieurs caractéristiques qui font d'eux un modèle écologique intéressant. Comparativement au milieu terrestre, l'organisation réticulée des rivières contraint les mouvements et la dispersion des organismes aquatiques le long des branches du réseau hydrographique. Conséquemment, les corridors de dispersion sont aisément identifiables et la distance parcourue par un organisme entre deux locations peut être facilement estimée (Peres-Neto 2004, Campbell Grant et al., 2007). De plus, les rivières révèlent une grande variabilité de type et de structure d'habitat (Baltz et Moyle, 1982; Ryder et Pesendorfer, 1989). De la tête à l'embouchure d'une rivière, plusieurs variables physiques présentent un gradient continu (*e.g.,* largeur, courant, profondeur, débit et température) (Vannote et al., 1980). À plus petite échelle, des liens sédimentaires (*i.e.,* unités naturelles des rivières déterminées principalement par l'organisation des tributaires et la taille du substrat) soulignent la nature discontinue des réseaux lothiques et sont souvent eux-mêmes composés d'une suite de mésohabitats tels des fosses et des seuils (Rice et al., 2001). Dans les rivières étudiées, trois mésohabitats pouvaient être distingués : les rapides, également désignés seuils, les droits, et les fosses aussi désignées mouilles. Les rapides sont caractérisés par un fort courant turbulent, un substrat de grande taille majoritairement des blocs métriques et un taux élevé d'échange gazeux avec l'atmosphère (Hynes, 1970; Allan, 1995). Les droits ont un courant intermédiaire, un substrat plus fin composé habituellement de galets ou de roches et moins d'échanges atmosphériques (Hynes, 1970; Allan, 1995). Les fosses ont un courant faible, un substrat très fin tel du gravier ou du sable souvent parsemé de branches et de macrophytes, et peu d'échanges atmosphériques (Hynes, 1970; Allan, 1995). Ces conditions environnementales contrastées entre les types d'habitat sont reconnues pour influencer la distribution des organismes (Seegrist et Gard, 1972; Schlosser, 1982; Poff et Ward, 1989;

Tetzlaff et al., 2005). Plusieurs organismes semblent adaptés à la moyenne d'une variable environnementale mais aussi au degré de variabilité de celle-ci (Nichols et al., 1976; Leggett et Carscadden, 1978; Tetzlaff et al., 2005).

Les écologistes sont de plus en plus conscients des problèmes associés aux processus spatiaux et ils réalisent comment le choix d'une échelle peut modifier la perception de la dynamique des communautés (Watson et Hillman, 1997 ; Deschênes et Rodríguez, 2007). Smith et Powell (1971) ont suggéré un cadre conceptuel pour envisager ce type de problématique. Ils proposent que les communautés soient le résultat d'une série de filtres de diverses natures agissant à différentes échelles spatiales, sélectionnant successivement les espèces adaptées aux conditions. À grande échelle, des traits physiologiques tels le type de métabolisme (*e.g.,* endotherme *versus* poïkilotherme) ou la tolérance au froid, peuvent limiter la distribution des organismes et d'importantes entités géographiques, comme une chaîne de montagne, peuvent contraindre la dispersion. À petite échelle, les variables environnementales décrivant le mésohabitat et le microhabitat peuvent être des facteurs déterminant la structure des communautés (Smith et Powell 1971). Ainsi, selon l'échelle ciblée différentes perceptions des processus structurant l'assemblage des communautés peuvent être obtenues. En écologie aquatique, il semblerait que les interactions biotiques soient des processus déterminant la structure des communautés, particulièrement à petite échelle (Huston, 1999; Pearson et Dawson, 2003). Au contraire, une grande échelle révèlerait plutôt une influence des facteurs abiotiques (Jackson et al., 2001). L'organisation hiérarchique des réseaux hydrographiques, où les mésohabitats sont nichés dans les rivières, qui sont elles-mêmes nichées dans des bassins versants, offre une structure spatiale particulière à différentes échelles. Par exemple, à petite échelle, comparer différents mésohabitats, comme des rapides, des droits et des fosses, devrait révéler une importante variabilité environnementale et ichtyologique. Augmenter l'échelle pour inclure l'ensemble de la rivière ou plusieurs rivières différentes, devrait accroître substantiellement la gamme de conditions environnementales et d'espèces rencontrées (Vannote et al., 1980). À grande échelle, des variations considérables peuvent être présentes entre les bassins versants s'ils sont façonnés par différents facteurs historiques et géographiques.

La répartition des organismes dans l'espace peut être définie à l'aide de plusieurs descripteurs biologiques, nous avons utilisé des *patrons de distribution*, des *patrons de cooccurrence* et des *patrons de diversité*. Les *patrons de distribution* permettent de contraster les caractéristiques entre les sites où une espèce est présente ou absente. Entre autres, cette démarche peut nous informer des préférences environnementales et d'un comportement de sélection d'habitat déterminant la distribution des espèces. Par contre, différents mécanismes peuvent produire des patrons de distribution semblables. Par exemple, autant la compétition que des préférences environnementales divergentes peuvent expliquer que les distributions de deux espèces ne se chevauchent pas. Les *patrons de cooccurrence* apportent de l'information supplémentaire sur la structure des communautés. En effet, la cooccurrence de paires d'espèces (*e.g.,* associations positives et négatives) permet d'élucider les mécanismes déterminant l'assemblage des espèces en communautés (Stone et Roberts, 1992; Peres-Neto et al., 2001; Sfenthourakis et al., 2005). Encore une fois, différents mécanismes peuvent générer ces patrons. Par exemple, des associations négatives peuvent être engendrées par la compétition, la prédation, l'isolation géographique, une capacité de dispersion limitée ou des préférences environnementales différentes. Des associations positives peuvent être causées par la facilitation ou des préférences environnementales similaires. Mais cette fois, à l'aide de modèles nulles, nous pouvons évaluer si l'environnement et les processus spatiaux sont responsables des patrons de cooccurrence, réfuter certaines hypothèses et ainsi raffiner notre compréhension des mécanismes structurant les communautés. Les *patrons de diversité* peuvent également améliorer notre compréhension de l'organisation des communautés. La diversité globale peut être partitionnée en composantes additives associées à différents niveaux hiérarchiques, tels que différentes échelles. Ce concept a été introduit par Whittaker en 1960 et a été modifié par la suite pour donner les composantes additives de la diversité globale γ en composantes présentes dans α échantillons et entre β échantillons (Lande, 1996; Pélissier et Couteron, 2007). Cette méthode a été utilisée pour étudier des patrons hiérarchiques de diversité dans des paysages agricoles (Wagner et al., 2000; Fournier et Loreau, 2001), des forêts tropicales (DeVries et al., 1997) et des forêts tempérées (Gering et al., 2003). On peut ainsi voir à quel niveau la diversité des espèces est la plus variable. Ces différents patrons ont été comparés entre trois différentes échelles spatiales (*e.g.,* section de mésohabitat, site de rivière et bassin versant).

1.2 Variabilité phénotypique : morphologie et capacité de nage

Les *patrons de différentiation phénotypique* des traits fonctionnels entre des espèces ou des populations est une avenue additionnelle qui a été proposée afin d'identifier des règles applicables à de plus larges ensembles d'organismes (Guisan et Thuiller, 2005; McGill et al., 2006). En effet, les traits fonctionnels peuvent apporter des détails additionnels sur les processus qui structurent les communautés. Les traits fonctionnels sont des caractéristiques décrivant la morphologie, la physiologie, l'histoire de vie ou le comportement des organismes. La moyenne et la variance des traits fonctionnels peuvent varier en fonction de gradients environnementaux. Lorsque les traits sont bien sélectionnés, leurs variations peuvent expliquer l'utilisation des ressources et les préférences environnementales des organismes. Ils peuvent également servir d'indicateur des mécanismes déterminant la composition (Wellborn et al., 1996; Leclerc et DesGranges, 2005), les patrons de cooccurrence (Armbruster et al., 1994; Silvertown, 2004; Stubbs et Wilson, 2004) et les patrons de différentiation phénotypique (McIntyre et al., 1999; Lavorel et Garnier, 2002). Ces variations phénotypiques entre les groupes peuvent être engendrées par la génétique et/ou la plasticité phénotypique. L'expression d'un trait est le phénotype et il est le fruit de l'interaction entre le génome et l'environnement. La relation directe entre le génome et le phénotype est bien connue et étudiée, mais ne permet pas d'expliquer la vitesse des réponses et l'amplitude des variations phénotypiques retrouvées dans certains écosystèmes. Une autre source de variation est l'effet indirect de l'environnement pouvant modifier rapidement le phénotype, indépendamment du génotype (Pigliucci, 2005). Ce processus nommé plasticité phénotypique peut être le premier pas vers le développement du polymorphisme qui peut résulter en divergences génétiques et finalement en spécialisation (West-Eberhard, 1989; Price et al., 2003; Pigliucci, 2005). Les comparaisons interspécifiques des phénotypes ont été critiquées parce que les divergences peuvent avoir évoluées avant ou après la spécialisation des espèces. Les variations intraspécifiques constitueraient le niveau taxonomique approprié afin de démontrer des compromis fonctionnels pouvant exister entre des phénotypes coexistants (Robinson et al., 1996). Différents régimes de sélection peuvent générer et maintenir une diversification phénotypique (Ehrlich et Raven, 1969; Rice et Hostert, 1993; Smith et Skúlason, 1996). Par exemple, la compétition semble pouvoir favoriser un déplacement de caractères et induire un polymorphisme (Gray et Robinson, 2002). La

variabilité phénotypique engendrée ainsi devrait réduire la compétition après la spécialisation de chaque groupe à une niche aux pressions de sélection distincte (Gray et Robinson, 2002). Selon Pigliucci (2005), un groupe d'individus ayant un important niveau de variabilité phénotypique devrait avoir de meilleures chances de survivre à un environnement variable. Cette tendance a été démontrée, du moins en partie, chez les plantes (Schlichting, 1986; Pigliucci et Kolodynska, 2002; Pigliucci, 2005), les poissons (Brinsmead et Fox, 2002), les amphibiens (Van Buskirk, 2002) et a été supportée par des modèles théoriques (Via et Lande, 1985; Scheiner, 1993; Scheiner, 1998; Sultan et Hamish, 2002).

Les traits retenus dans cette étude sont la morphologie et la capacité de nage des poissons de rivières puisqu'ils pouvaient être évalués au niveau des populations, sont reconnus pour être variables et avoir un rôle écologique. Les caractéristiques morphologiques peuvent contraindre les habiletés des poissons à utiliser des types d'habitat, (Snorrason et al., 1994), acquérir des ressources (Brönmark et Miner, 1992), tolérer des conditions locales, éviter la prédation (Brönmark et Miner, 1992) et particulièrement nager efficacement (Webb, 1984). Fonctionnellement, la forme optimale devrait être celle qui maximise la poussée et minimise la traînée (*i.e.,* résistance ou force s'opposant au mouvement d'un corps) (Webb, 1984). Différentes formes impliquent différentes capacités et différents coûts de nage (Webb, 1982; Webb, 1984). Les poissons fusiformes tendent à être de meilleurs nageurs contre un courant soutenu, peuvent parcourir de longues distances et faire face à un courant important à faibles coûts. Au contraire, une forme trapue augmente la capacité d'accélération et la manœuvrabilité dans un habitat complexe (Webb, 1982 ; Taylor et McPhail, 1985). De longues nageoires pectorales situées ventralement augmentent la manœuvrabilité (Webb, 1984), tandis que de plus petites diminuent la traînée (Drucker et Lauder, 2003). Des variations morphologiques ont été retrouvées entre diverses populations de poissons en fonction de l'habitat utilisé: lac *versus* rivière, étang *versus* rivière ou pélagique *versus* littoral (Robinson et al., 1996; Brinsmead et Fox, 2002; Robinson, 2000; Langerhans et al., 2003). La majorité des recherches se sont concentrées sur les lacs et ont évalué le dimorphisme présent entre les populations appartenant à la zone pélagique et à la zone littorale. Il semble que les poissons de la zone pélagique doivent parcourir de longues

distances pour éviter la prédation et s'alimenter sur des ressources dispersées. Au contraire, les poissons de la zone littorale ont accès à un habitat plus complexe, une plus grande accessibilité aux ressources alimentaires et à des refuges offrant une protection accrue. Les poissons de la zone pélagique ont donc des proies, un comportement alimentaire et une demande de nage différents des poissons de la zone littorale (McLaughlin et Grant, 1994; Bourke et al., 1997; Robinson et Parsons, 2002). Robinson et Parsons (2002) ont résumé certaines divergences morphologiques et leurs avantages associés à ces deux zones écologiquement distinctes (Robinson et Parsons, 2002). En comparaison aux poissons de la zone littorale, ceux de la zone pélagique ont une silhouette plus fusiforme, une tête plus effilée et de plus petites nageoires (Robinson et Parsons, 2002). Ce patron de différentiation morphologique entre les populations des zones pélagiques et littorales a été supporté du moins en partie pour plusieurs espèces : le crapet soleil *(Lepomis gibbosus)* (Robinson et al., 1993; Robinson et al., 1996; Jastrebski et Robinson, 2004), le crapet arlequin *(Lepomis macrochirus)* (Robinson et al., 1993), le grand corégone *(Coregonus clupeaformis)* (Lindsay, 1981), l'épinoche à trois épines *(Gasterosteus aculeatus)* (Schluter et McPhail, 1992; Schluter et Nagel, 1995; Robinson, 2000) et le guppie *(Poecilia reticulata)* (Robinson et Wilson, 1995). La présence d'un prédateur peut également provoquer des variations phénotypiques. Par exemple, la présence du grand brochet du nord (*Esox lucius*) semble modifier la morphologie des populations de carpes (*Carassius carassius*) avec lesquelles il co-occurre. Les populations de carpes co-occurrant avec le grand brochet semblent plus trapues ce qui serait une adaptation afin de réduire la prédation (Brönmark et Miner, 1992). Les patrons de différentiation phénotypique des poissons de rivières ont été peu étudiés et pour un nombre limité d'espèces (Beacham et Murray, 1989; McLaughlin et Grant, 1994; McLaughlin et Noakes, 1998).

1.3 Ecologie des espèces

Durant l'échantillonnage, 23 espèces ont été capturées, dont 17 étaient en nombre suffisant pour cette étude.

La famille des cyprinidés est celle dont le plus d'espèces ont été rencontrées. Le mulet à cornes (*Semotilus atromaculatus*), la ouitouche (*Semotilus corporalis*), le mulet perlé (*Margariscus margarita*), le naseux des rapides (*Rhinichthys cataractae*), le tête-de-boule (*Pimephales promelas*), le méné à nageoires rouges (*Luxilus cornutus*) et le bec-de-lièvre (*Exoglossum maxillingua*) ont été capturés. Les cyprinidés, communément appelés ménés, sont de petits poissons mesurant habituellement moins de 10 cm, bien que des mulets peuvent atteindre jusqu'à 40 cm (Bernatchez et Giroux, 2000). Les ménés se nourrissent majoritairement d'insectes, de zooplancton et de matière végétale. La fraie a lieu entre mai et août. Chez quasiment toutes les espèces, à l'exception du naseux des rapides et du mulet perlé, les mâles construisent des nids et deviennent territoriaux durant cette période. Les cyprinidés sont habituellement très abondants et constituent la base de l'alimentation des piscivores. Ils sont grégaires et forment souvent des bancs (Bernatchez et Giroux, 2000).

Des centrarchidés, tels le crapet soleil (*Lepomis gibbosus*), le crapet de roche (*Ambloplites rupestris*) et l'achigan à petite bouche (*Micropterus dolomieu*), ont également été capturés. Ces espèces sont aplaties latéralement et ont une forme de disque. Les crapets peuvent mesurer jusqu'à 25 cm, tandis que l'achigan peut facilement dépasser 40 cm. Ces espèces fraient entre mai et août. Durant cette période, les mâles sont agressifs envers les intrus, creusent et gardent des nids un certain temps suivant l'éclosion des œufs. La diète des centrarchidés est composée d'insectes, de mollusques, de zooplancton, d'écrevisses et de petits poissons (Bernatchez et Giroux, 2000).

Deux espèces de salmonidés ont également été étudiées, la truite mouchetée ou omble de fontaine (*Salvelinus fontinalis*) et la truite brune (*Salmo trutta*). Ces espèces mesurent entre 25 et 35 cm, mais peuvent parfois dépasser 50 cm. Ces poissons fraient tardivement entre octobre et décembre dans des eaux peu profondes à la tête des cours d'eau où la femelle creuse un nid dans le gravier. Ils ont une alimentation variée, composée de zooplancton, de proies benthiques, d'insectes, de crustacés et de poissons (Bernatchez et Giroux, 2000). Il est

à noter que dans la région étudiée, de nombreuses populations d'omble de fontaine sont ensemencées et pêchées.

Appartenant à la famille des percidés, la perchaude (*Perca flavescens*) mesure en moyenne entre 10 et 25 cm. La fraie a lieu entre avril et mai dans des zones peu profondes pourvues de végétation, de racines et de branches. C'est un poisson grégaire qui se nourrit surtout d'insectes, d'invertébrés et de petits poissons. La perchaude est une proie, mais aussi une compétitrice de plusieurs prédateurs et est exploitée commercialement. De la même famille, le fouille-roche zébré (*Percina caprodes*) est un poisson de forme cylindrique au museau effilé. Il est le plus grand des dards de la région et mesure entre 9 et 20 cm. Il fraie entre juin et juillet en eau peu profonde. Ce poisson se nourrit d'insectes et de petits crustacés, qu'il débusque en retournant des pierres avec son museau (Bernatchez et Giroux, 2000).

De la famille des umbridés, l'umbre de vase (*Umbra limi*) est un petit poisson qui mesure entre 5 et 10 cm. Il reste habituellement sur le lit des rivières à fond vaseux recouvert de matière organique et de macrophytes, dans lequel il s'enfouit pour se cacher ou résister à la sécheresse. La fraie a lieu au début du printemps. Cette espèce a la particularité de pouvoir respirer l'oxygène atmosphérique (Bernatchez et Giroux, 2000).

Un catostomidé, le meunier noir (*Catostomus commersoni*) est un poisson robuste mesurant habituellement entre 30 et 50 cm. Il possède une bouche infère munie de lèvres charnues recouvertes de papilles. Il se retrouve dans une large gamme de condition: eau chaude ou froide, fond rocheux ou vaseux avec ou sans végétation et à courant lent ou fort. Au moment de la fraie, entre mai et juin, les adultes se rassemblent pour remonter de petits cours d'eau graveleux à courant modéré ou sur la rive des lacs. Le meunier se nourrit sur le fond majoritairement d'invertébrés benthiques. Les jeunes de cette espèce font partie de la diète de plusieurs poissons piscivores (Bernatchez et Giroux, 2000).

De la famille des ictaluridés, la barbotte brune (*Ameiurus nebulosus*) a un corps massif et mesure entre 20 et 35 cm. Elle est dépourvue d'écaille, possède quatre paires de barbillons et des épines aux nageoires pectorales et à la nageoire dorsale. Au moment de la fraie, entre mai et juin, les parents creusent un nid et gardent les jeunes durant plusieurs semaines après l'éclosion. Surtout nocturne et benthique, la barbotte a un régime omnivore et s'alimente sur le fond de mollusques, de débris, d'insectes, d'écrevisses, de vers, d'algues et d'œufs de poissons. C'est une espèce très résistante aux contaminants, qui a la particularité de pouvoir respirer par la peau et de s'enfouir dans la vase pour résister aux sécheresses (Bernatchez et Giroux, 2000).

PREMIER CHAPITRE

MULTI-SCALE INFLUENCES OF THE ENVIRONMENT AND SPATIAL STRUCTURE ON PATTERNS OF DISTRIBUTION, CO-OCCURRENCE AND DIVERSITY OF RIVERINE FISH

L'influence multi-échelle de l'environnement et de la structure spatiale sur les patrons de distribution, de cooccurrence et de diversité des poissons en rivière

ABSTRACT

We evaluated the multi-scale structure of riverine fish community by quantifying the presence-absence of 17 species and environmental variables in a nested sampled design consisting of 143 sections representing the mesohabitats, nested within 38 stream sites that were themselves nested across 3 watersheds, in the Laurentian region of Québec, Canada. The specific objectives were: (1) Assess patterns in habitat selection among species according to their environmental preferences; (2) Partition the variability of both environmental conditions and species distributions, as well as the relationships between them, across three nested spatial scales (*e.g.*, watershed, stream site and mesohabitat section); (3) Model the spatial structure across sampling units based on water course distances using continuous spatial predictors representing non-directional (total distance) and directional (upstream and downstream distance) variations; (4) To estimate the importance of environmental conditions and spatial descriptors on species co-occurrence across three nested spatial scales and (5) Partition the global diversity into hierarchical additive components associated to the three nested spatial scales. We showed that species distributions were linked to the environment and that 60% of the species presented some level of habitat preference. Species distributions and environmental conditions were similar throughout watersheds, while species distributions varied mostly among sites and environment mostly across sections. Presence of species and environmental conditions were best predicted by total stream distance among sites. Species negative co-occurrences were explained by species environmental affinities and spatial structure, while species positive co-occurrence remained important at small scales after controlling for environment and space. The hierarchical partitioning of beta-diversity suggested a different organization of the relationship among scales.

Keywords: co-occurrence, distribution, diversity, environment, fish, multi-scale, multi-species, spatial structure, stream.

L'influence de l'environnement et de la structure spatiale à différentes échelles sur divers descripteurs biologiques décrivant la distribution de 17 espèces de poissons des rivières a été déterminée. Les résultats ont souligné l'importance de l'échelle choisie en ce qui concerne la variabilité des conditions environnementales et de la distribution des poissons, en plus des patrons de cooccurrence et de diversité. Sur les 17 espèces retenues pour cette partie, 60% a sélectionné un type d'habitat particulier. La distance par voie d'eau totale entre les sites est celle qui a modélisé le plus fidèlement la structure spatiale de l'environnement et la distribution des espèces. L'environnement et la structure spatiale ont expliqué significativement les patrons de distribution et de cooccurrence. De plus, notre perception des patrons de diversité est affectée par le choix d'une approche hiérarchique ou non-hiérarchique.

Mots clés: cooccurrence, distribution, diversité, environnement, multi-échelle, multi-espèce, poisson, rivière, structure spatiale.

CHAPITRE I

MULTI-SCALE INFLUENCES OF THE ENVIRONMENT AND SPATIAL STRUCTURE ON PATTERNS OF DISTRIBUTION, CO-OCCURRENCE AND DIVERSITY OF RIVERINE FISH

2.1 Introduction

2.1.1 An overview of distributional patterns

The mechanisms that drive natural assemblages and are responsible for selecting species to form local communities are one of the oldest, yet actual important and dominant themes in ecology (Pulliam and Danielson, 1991; Remes, 2000; Morris, 2003). Until recently, most ecologists and conservation biologists have sought to explain differences in species distribution and community structure by measuring the influence of the environment on local species interactions at small scales. Indeed, a great component of ecological research has focused mainly on the relationships among physical conditions, local populations and species interactions at small scales using experiments, mesocosms and statistical modelling of species distributions (Lotka, 1925; Voltera, 1926; Gause, 1934; Hutchinson, 1957; MacArthur and Levins, 1967). More recently, ecology has experienced what Kingsland (1985) referred to as the «eclipse of history» which generated a fundamental transformation of the discipline. Macroecology emerged and brought new issues and concepts. The

combined effects of environmental, geographical and historical processes were brought in to explain species distribution patterns across different temporal and spatial scales (Ricklefs, 1987). In many systems, both local and regional processes appear to jointly regulate diversity and community composition (Burke and Grime, 1996; Tilman, 1997; Shurin et al., 2000; Resetarits, 2005). However, the relative contributions of small *versus* large scales processes and the relevant scale at which mechanisms drive spatial variation in community structure remain poorly understood (Ricklefs, 1987; Caswell and Cohen, 1993; Huston, 1999; Lawton, 1999; Srivastava, 1999; Gaston, 2000).

2.1.2 Filter theory and spatial variation in fish communities

Smith and Powell (1971) suggested an appealing conceptual framework to address these questions. They proposed that local communities are the result from multiple selective pressures ranging from broad range effects to finer scale influences. They described their framework as a series of filters that sequentially select species starting from the global pool of potential colonizers until only the species found locally (*i.e.*, small scale) are left (fig. 2.1). These filters encompass different physiological, geographical and evolutionary mechanisms acting at different scales: worldwide, regional and local. For instance, some studies have suggested that small scale is associated to a greater importance of competition, while large scale studies emphasize the importance of abiotic control (Jackson et al., 2001; Huston, 2002; Pearson and Dawson, 2003). Although the concept of spatial scales (Smith and Powell, 1971) has greatly changed our understanding of the processes structuring communities, they also brought attention to important analytical features. Both species distribution and environment tend to be spatially structured by dispersal and the geographic organisation of local habitats, respectively. These spatialized processes may produce false positive or false negative associations between species distributions and environmental characteristics (Legendre and Legendre, 1998). This is caused by spatial autocorrelation, which refers to the lack of independence among the error components of model of species distributions due to the spatial structure of sampled sites. Spatial processes that influence response and predictive variables may generate autocorrelation in both sets of variables, producing apparent concordance between them due to geographic (rather than functional) relatedness and thus elevated type I

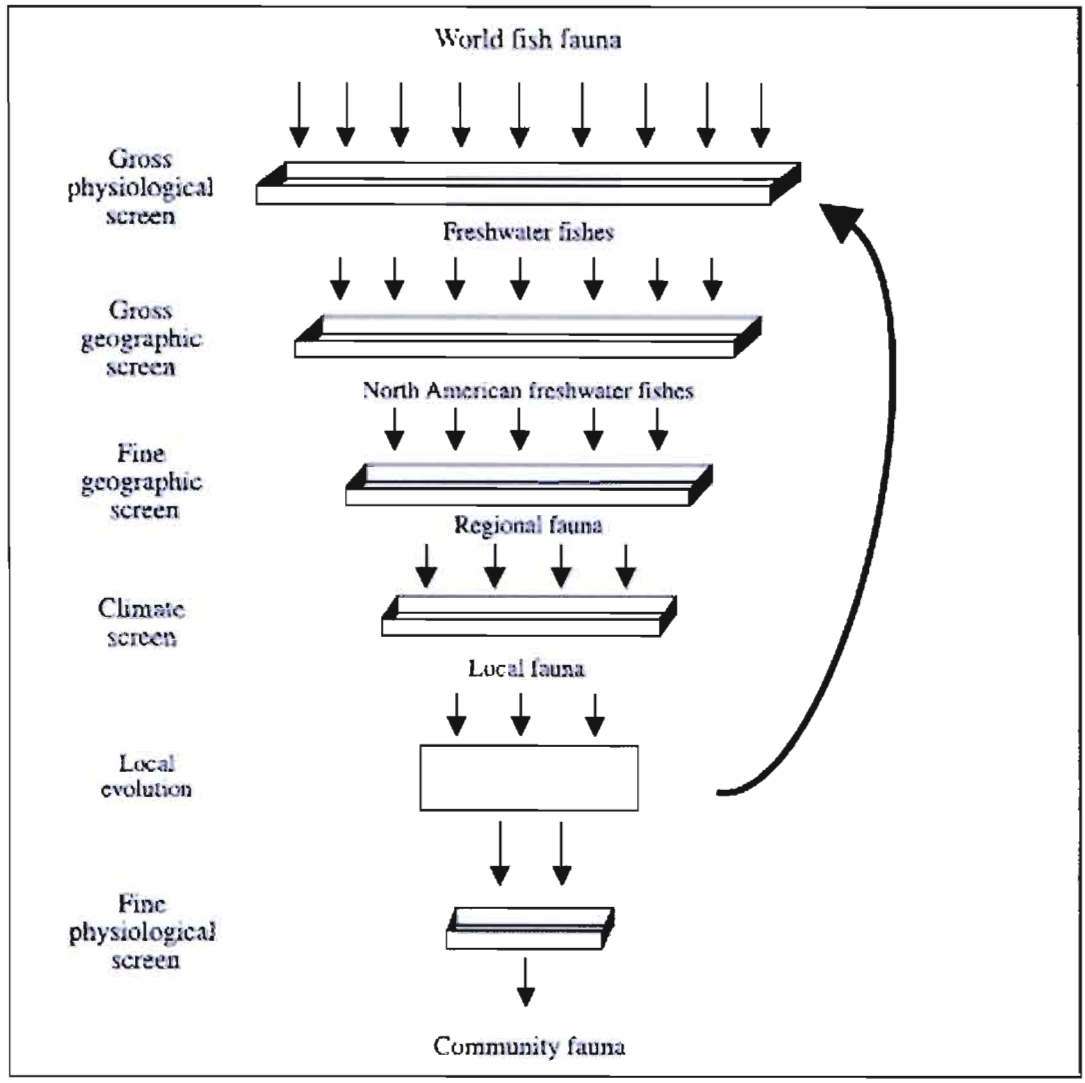


Figure 2.1 A depiction of the successive filters, which select fish species from large to small scales, from the global pool of species to compose local communities. This version of the framework is an adaptation from Smith and Powell (1971) by Jackson et al. (2001).

error rates in statistical analyses (Legendre, 1993; Legendre and Legendre, 1998). By accounting for the spatial structure and autocorrelation patterns, two tasks can be achieved: 1) the bias in statistical analyses and models can be controlled and (2) the importance of missing spatialized processes such as dispersal, habitat connectivity, local species adaptation and unmeasured environmental variables can be estimated. In sum, by considering spatial predictors explicitly in the analysis of species distributions, we can evaluate if the relationship between species distribution and environmental characteristics are truly functional, measure the importance of spatial drivers and assess whether species variation is consistent or not across multiple spatial scales.

2.1.3 Why study stream-fish assemblages?

Stream systems have many characteristics that make them well-suited to study the multi-scale effects of different processes on the organization of species assemblage. Streams have a strong longitudinal gradient and their physical characteristics are highly variable in space and time (Vannote et al., 1980; 1989; Acreman and Dunbar, 2004). The reticulate organization of streams system limits the movement of fish among the branches of the system. Consequently, the dispersal corridors and the distance travelled by an organism among sites may be estimated with great accuracy (Peres-Neto, 2004; Campbell Grant et al., 2007). Fish respond to the environmental conditions encountered in streams (Seegrist and Gard, 1972; Poff and Allan, 1995; Tetzlaff et al., 2005) and appear to be not only adapted to the mean, but also to the degree of environmental variability observed in these systems (Leggett and Carscadden, 1978; Tetzlaff et al., 2005). Streams are often organized as a sequence of contrasting habitats such as riffles, runs and pools, providing replicated conditions regarding habitat types at different spatial scales, from mesohabitat (*e.g.,* riffle, run and pool) to watersheds. The hierarchical nature of streams in which mesohabitats are nested into streams, which are themselves nested into watersheds, should shed light on the relationships among local environmental factors, spatial structure and species distribution across spatial scales. For instance, in the particular case of stream systems, habitat variability exists over a range of spatial scales. At small scale, if different mesohabitat types (*e.g.,* riffle, run and pool) are

compared, environmental conditions and species composition should exhibit important variability. Increasing the scale to include multiple reaches and streams of different geomorphometry should lead to a substantial increase in the range of conditions within the system. Moreover, considerable variations could be observed among watersheds if they are structured by different historical and/or geographical factors since they may be responsible for determining the regional pool of species from which local communities can be selected.

2.1.4 Species distribution, co-occurrence and diversity

Often, different mechanisms can lead to similar patterns of distribution. Species co-occurrences allowed us to distinguish the effect of environmental conditions, spatial structure and species interactions (Stone and Roberts, 1992; Peres-Neto et al., 2001; Sfenthourakis et al., 2005). For instance, negative co-occurrences may be caused by species interactions (*e.g.,* competition and predation), spatial processes (*e.g.,* isolation, dispersal) or different habitat requirements, whereas positive co-occurrences may be promoted by species interaction such as facilitation (*i.e.,* a species benefit from the presence of another) or similar environmental requirements. Patterns of diversity can also improve our understanding of community structure by partitioning the variability into additive components related to different hierarchical levels, such as spatial scales. The concept of diversity comes from Whittaker (1960) and has been adapted in order to generate additive partitions of the total γ species diversity (total species richness in a landscape) into components found within samples (α component or local richness) and among samples (β diversity; Lande, 1996; Pélissier and Couteron, 2007; Veech and Crist, 2007). Examples of additive partitions used to analyze hierarchical patterns of species diversity can be found for agricultural (Wagner et al., 2000; Fournier and Loreau, 2001), tropical (DeVries et al., 1997) and temperate landscapes (Gering et al., 2003).

2.1.5 Chapter objectives

Here we assess patterns of stream fish distribution, co-occurrence and diversity, contrasting the importance of environmental suitability and spatial structure across different spatial scales, from mesohabitats to entire watersheds. The specific objectives are as follows: (1) Assess patterns in habitat selection among species according to their environmental preferences; (2) Partition into explained fractions the variability of both environmental conditions and species distributions, as well as their relationships, across three nested spatial scales (*e.g.,* watershed, stream site and mesohabitat section); (3) Model the spatial structure among sampling units based on water course distances using spatial predictors representing non-directional (total distance) and directional (upstream and downstream distance) variations; (4) Estimate the importance of environmental conditions and spatial descriptors on species co-occurrence across three nested spatial scales and, (5) Partition the overall diversity into hierarchical additive components associated to the three nested spatial scales.

2.2 Methodology

2.2.1 Study area

We sampled 39 stream sites situated in three distinct watersheds in the Laurentian region of Québec, Canada, (fig. 2.2). These watersheds are all connected through the Ottawa River that flows towards the St-Lawrence River and are located between 45°47' and 46°22' North, and 73°56' and 72°37' West, roughly encompassing 1700 km^2. This region is characterized by a temperate climate, urbanized areas especially in the South, as well as boreal forests and mountains mainly in the North. Sampling was conducted from June 8 to August 15, 2007. Sites were visited once and sampling performed within the day. Average sites length was 130 meters (m) and the average width was 7 m. Sites were divided into three to five sections corresponding to one of the mesohabitats (*e.g.,* riffle, run and pool). Average section length was 35 m. We excluded one site where no fish were encountered and ended up with 143 sections distributed across 38 sites located in three watersheds. Therefore, the sampling design represents three hierarchical spatial scales, (*i.e.,* 1 - sections representing the mesohabitat which are nested into 2 - sites representing stream, which are themselves nested into 3 - watersheds, which corresponds to the largest scale). Throughout the text, this hierarchical arrangement will be referred to as nested spatial scale or structure. Fish species were identified and environmental variables were characterized at the smallest nested spatial scale (*i.e.,* mesohabitat section).

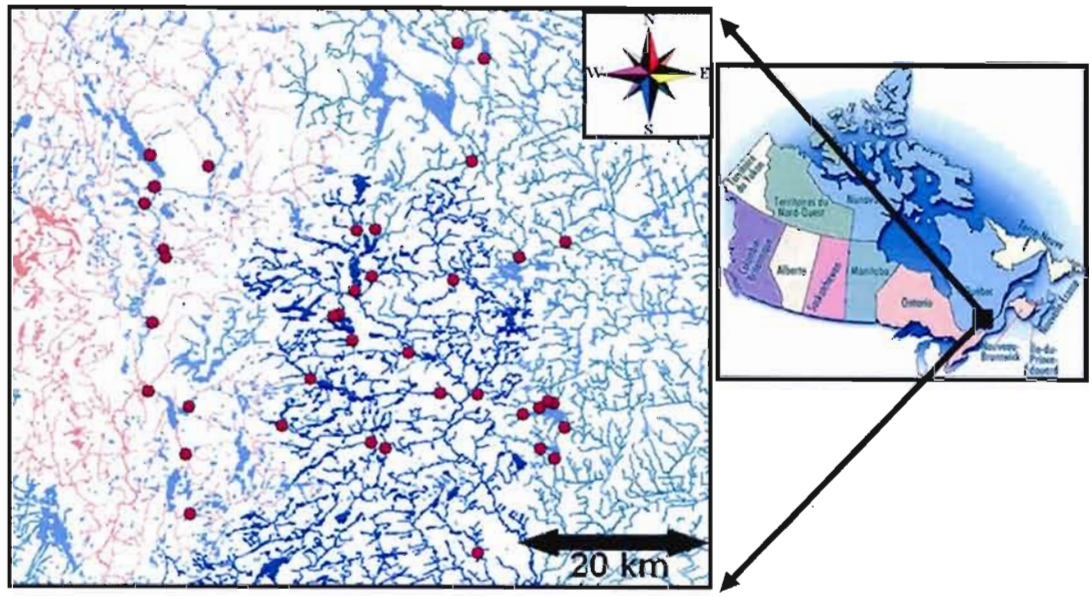


Figure 2.2 Map of the studied region located in Laurentian region of Québec, Canada. The 39 sites are represented by circles. The watershed of the Rivière Rouge is on the west side in red, watershed of the Rivière du Nord is in the middle in blue and watershed of the Rivière Ouareau is on the east side in green.

2.2.2 Environmental characteristics

For each of the 143 sections, we measured or visually estimated environmental variables that were considered potentially important in driving fish distribution (tabl. 2.1). The environmental variables, their resolution and code are listed (tabl. 2.1). Habitat type (*e.g.,* riffle, run and pool), land use (*e.g.,* residential, commercial, industrial, forest), vegetation of the bank, stream and bank slopes, presence of channelization structures (*e.g.,* rectification channels), road and tributary, percentage of substrate type (*e.g.,* sand, gravel, rock), water temperature, number of submerged tree branches (*i.e.,* minimum diameter of 5 cm), number of residences, percentage of macrophyte coverage, section's length and sampling date were evaluated. Stream cross-sectional depth, width and water velocity were measured every 1 m and longitudinally at 5 m intervals. Water velocity was measured in the middle and at the bottom (*i.e.,* 3 cm above the stream bed) of the water column using a flow probe (Global Water, FP-101). For these measures and the substrate type, a coefficient of variation (VC) by section was calculated. We coded nominal variables (tabl. 2.1) as dummy variables. Since environmental variables are in different units, they have been standardized prior to analyses to remove their physical dimension (Legendre and Legendre, 1998).

Table 2.1

List of the environmental variables measured in each section, their code and resolution

Variable		Code	Resolution
Habitat type	Pool section	Pool	Nominal
	Riffle section	Riffle	Nominal
	Run section	Run	Nominal
Landuse	Industrial and commercial zone	I-C	Nominal
	Forest zone	For	Nominal
	Residential zone	Res	Nominal
Type of vegetation of the bank		Vege	Nominal
Slope of the bank		Sban	Nominal
Slope of the stream		Sstr	Nominal
Channelization structures		AS	Presence-Absence
Presence of road		Road	Presence-Absence
Presence of tributary		Trib	Presence-Absence
Substrate type	Clay	Clay	Quantitative
	Silt	Silt	Quantitative
	Sand	Sand	Quantitative
	Pebbles (2-32mm)	Peb	Quantitative
	Gravel (32-64mm)	Grav	Quantitative
	Cobble (64-250mm)	Cob	Quantitative
	Rocks (250-1000mm)	Roc	Quantitative
	Boulder (>1m)	Boul	Quantitative
	Bedrock	BedR	Quantitative
	Substrate variation coefficient	SVC	Quantitative
Water temperature		Temp	Quantitative
Number of residences		Buil	Quantitative
Number of tree branches		Bra	Quantitative
Percentage of macrophyte cover		Mac	Quantitative
Length of the section		Len	Quantitative
Average depth		AD	Quantitative
Depth variation coefficient		DVC	Quantitative
Average width		AW	Quantitative
Width variation coefficient		WVC	Quantitative
Average bottom flow		ABF	Quantitative
Bottom flow variation coefficient		BFVC	Quantitative
Average middle flow		AMF	Quantitative
Middle flow variation coefficient		MFVC	Quantitative
Sampling date		Sam	Quantitative

2.2.3 Fish sampling

Fish within sections were sampled using electrofishing with pulsed current (Smith & Root, LR-24). Because we were only interested in species presence and absence, only one pass was conducted while going upstream throughout the site in a zigzag movement removing all fish encountered. Note that sections were not blocked due to time and logistic constraints. Sites were not studied in sufficient detail to ascertain whether the collected fish represented viable populations but we assumed that all individuals were from established populations. Overall, more than 4000 fish belonging to 23 species were captured. The 17 most common species belonging to seven families were retained for analyses: creek chub (*Semotilus atromaculatus*), pumpkinseed sunfish (*Lepomis gibbosus*), common shiner (*Luxilus cornutus*), rock bass (*Ambloplites rupestris*), cut lips (*Exoglossum maxillingua*), brook trout (*Salvelinus fontinalis*), the central mudminnow (*Umbra limi*), the white sucker (*Catostomus commersoni*), brown bullhead *(Ictalurus nebulosus* or *Ameiurus nebulosus*), yellow perch (*Perca flavescens*), smallmouth bass (*Micropterus dolomieu*), fallfish (*Semotilus corporalis*), longnose dace (*Rhinichthys cataractae*), fathead minnow (*Pimephales promelas*), pearl dace (*Margariscus margarita*), logperch (*Percina caprodes*) and brown trout *(Salmo trutta*). These species were present in at least 5% of the 143 sections (tabl. 2.2).

Table 2.2

Species common name, family, species code (*e.g.*, first two letters of their scientific name), percentage of occurrence by sites and by sections for the seventeen species listed by their percentage of occurrence by sections

Species common name	Family	Species code	% occurrence by sites	% occurrence by sections
Creek chub	Cyprinidae	SeAt	74	55
Pumpkinseed sunfish	Centrarchidae	LeGi	74	46
Common shiner	Cyprinidae	NoCo	58	43
Rock bass	Centrarchidae	AmRu	55	43
Cut lips	Cyprinidae	ExMa	53	43
Brook trout	Salmonidae	SaFo	34	30
Central mudminnow	Umbridae	UmLi	47	29
White sucker	Catostomidae	CaCo	55	28
Brown bullhead	Ictaluridae	AmNe	53	24
Yellow perch	Percidae	PeFl	42	23
Smallmouth bass	Centrarchidae	MiDo	34	20
Fallfish	Cyprinidae	SeCo	32	20
Longnose dace	Cyprinidae	RhCa	29	16
Fathead minnow	Cyprinidae	PiPr	21	13
Pearl dace	Cyprinidae	MaMa	13	09
Logperch	Percidae	PeCa	11	05
Brown trout	Salmonidae	SaTr	08	05

2.2.4 Statistical analyses

2.2.4.1 Habitat selection

Species environmental preferences were assessed as follows. Sections used by each species were separated by mesohabitat type (*e.g.*, riffle, run and pool) and percentages of used habitat were calculated as the ratio between used and total (*i.e.*, used and non-used) sections per mesohabitat (tabl. 2.3). Species habitat selection was assessed using a chi-square analysis on a contingency table corresponding to the number of habitats used and non-used for each mesohabitat. This test compared the observed value to an expected value under an equal distribution of mesohabitats (*i.e.*, absence of preference; Scherrer, 1984). Chi-square values and associated probabilities were obtained for each species using the function chisq.test in the stats package of the R software. When a significant association was encountered (*i.e.*, significant chi-square), we calculated a Freeman-Tukey deviate for each cell (Sokal and Rohlf, 1995) to assess which habitats were significantly selected and avoided (tabl. 2.3).

2.2.4.2 Contrasting species distribution variability versus environmental variability across nested spatial scales: watershed, site and section

A question that is often disregarded by studies that consider species distributions and environment across different scales is how their variability is structured across scales. In this study, the variability of both species distribution and environmental conditions can be linked to the different nested spatial scales assessed (*e.g.*, watershed, site and section). In order to quantify the components of variability across these scales, we used a variation partitioning scheme based on partial Redundancy Analysis (RDA) (Borcard et al., 1992; see Peres-Neto et al., 2006 for a recent review of the method), following an approach similar to Reyjol et al. (2008). This analysis partitions the species variability explained by multiple sets of explanatory variables into unique and shared fractions of variation (Borcard et al., 1992; Legendre and Legendre, 1998; Peres-Neto et al., 2006). Watersheds and sites were coded as Helmert's contrasts to be used as predictor variables. In this case, the variation partitioning

estimates the unique fractions ([a]) and ([c]) that correspond to the variability linked exclusively to the watershed and the site, respectively, the fraction ([b]) that is common to both scales due to an unbalanced design given that the number of sites per watershed varied and the fraction ([d]) which represents residuals and corresponds to variation across all sections. Sections represent the smallest sampling unit and their variability cannot be tested as samples were performed only once in each section; hence they are represented by the residuals fraction ([d]). Fractions were adjusted by their number of predictors (Peres-Neto et al., 2006). The significance of the watershed ([a]) and site ([c]) fractions were tested by 999 permutations (see Legendre and Legendre, 1998 for details). These analyses were performed for each species, the whole community and environmental conditions using Matlab functions for variation partitioning (Peres-Neto et al., 2006). To facilitate the link between the analysis and their output results, I will indicate throughout the methods section where the results of particular methods are shown. The results of this analysis are shown in table 2.4.

2.2.4.3 Linking species distributions and environmental variability

Since numerous environmental variables were sampled, a stepwise forward selection was performed to retain the environmental variables that were significantly linked to species distributions (function forward.sel written by Dray in the R software; selected variables are shown in table 2.5). The relationship between the selected environmental variables and species distributions was visualised by an RDA biplot (fig. 2.3). In biplots, two types of scaling can be considered, either based on a distance or correlation scaling, where each type evokes a different interpretation of the relationships among variables (see Legendre and Legendre, 1998 for details). When eigenvalues are nearly equal, which is the case here, both scalings lead to very similar biplots. This analysis was performed with the rda function in the vegan package of the R software and the significance of predictors on each axis was tested using permutations tests based on 999 permutations.

2.2.4.4 Linking species distributions and environmental variability across nested spatial scales: watershed, site and section

After quantifying species distribution and environmental variability across scales, the variability of the species distribution that was explained by the environment was partitioned across nested spatial scales (*e.g.,* watershed, site and section). Mean values of the significant environmental variables related to species distributions (tabl. 2.5) were calculated for each site to estimate the variability in species distribution explained by the environment at the site scale. For each section, residual values (*i.e.,* section values minus the mean of their respective site) for each significant environmental variable were calculated. Note that these residuals are related to differences among sections since the difference in species distribution and environment is zero at the watershed level (tabl. 2.4). Following, the site means and section residuals were entered in a variation partitioning scheme. This allowed the quantification of the distribution variability explained by the environment at the site (fraction [a]) and section (fraction [c]) scales. These analyses were performed for each species and the whole community in Matlab and its results are presented in table 2.6.

2.2.4.5 Continuous spatial predictors: eigenvectors maps

Several methods are available for modelling the spatial structure of a variable (Fortin and Dale, 2005). Some can be adapted to represent the spatial structure of stream systems, allowing to measure spatial processes such as autocorrelation, isolation and dispersion when assessing the relationship between species distribution and environmental characteristics. One of them is eigenvector maps, which are eigenvector functions representing the spatial structure among sampling units (Borcard and Legendre, 2002; Dray et al., 2006; Griffith and Peres-Neto, 2006). The analysis breaks the global spatial structure into orthogonal variables representing the spatial structure present at different scales in the sampling design. First, the distance matrix is truncated at a threshold calculated by a minimum spanning tree (*i.e.,* the threshold is the maximum distance from the tree, the one that keeps all sites connected). Distances smaller or equal to the threshold are kept whereas values greater than the threshold are replaced by four times the threshold (Dray et al., 2006). Then, a principal coordinate

analysis is conducted on the truncated matrix and the eigenvectors associated to the positive eigenvalues are selected. These eigenvectors represent the spatial descriptors associated to positive autocorrelation corresponding to different scales and can be included in statistical analyses in order to measure the amount of variation in data due to spatial variation. Three types of water course distances were considered to generate spatial predictors representing non-directional (total distance) and directional (upstream and downstream distance) variation; in order to assess which one provided the best set of predictors namely, the total, upstream or downstream distances and, the best set was used in all subsequent analyses. These distances were measured using ArcView 8.3. Since the distance among sections was very small, only water course distances among stream sites were considered. The distance matrix that had the strongest association with species distributions and environmental variables was determined by variation partitioning using the function varpart in the vegan package of the R software (tabl. 2.7). The variation in species distribution was partitioned between the environment and the spatial descriptors associated with the best model (fig. 2.4). Eigenvectors that were most significantly related to species distribution were assessed via forward selection (tabl. 2.8). Eigenvectors maps will be referred to as continuous spatial structure, in contrast to the nested spatial scale or structure (*i.e.*, watershed, site and section).

2.2.4.6 Species co-occurrence across nested spatial scales: watershed, site and section

Variability of species co-occurrence across nested spatial scales was assessed using null models. Null models seek for structured patterns in species co-occurrences by contrasting observed species co-occurrence patterns to randomized data, which generates null distributions under the expectation of no association among species (Gotteli, 2000; Gotteli, 2001). Then, the observed statistic is compared to the null distribution to assess its significance (*i.e.*, presence of co-occurrence patterns). There are a number of randomization procedures (Anderson and Legendre, 1999; Gotteli, 2000; Anderson, 2001; Gotteli, 2001; Anderson and TerBraak, 2003). The algorithm used here kept the species occurrences constant (*i.e.*, number of sites occupied), but allowed the site richness to vary (Gotteli, 2001). Ecologically, this means that sites can contain a variable number of species due to colonization-extinction dynamics in the landscape. Two co-occurrence statistics were used:

the C-scores measures negative co-occurrences among species and is maximum when half of the sites are occupied by species A and the other half occupied by species B and, positive co-occurrences were assessed by the T-score, which is maximum when half of the sites is occupied by both species and the other half is not occupied by either species (Stone and Roberts, 1992).

A series of null models were compared to the occurrence data. The first type of null model was unconstrained in the sense that species presence/absence values were permuted across sections assuming equal habitat suitability and no continuous spatial structure. Note however, that permutations were performed within the different nested spatial scales (*i.e.,* watershed, site and section) in order to assess the importance of species associations at each of these nested scales. Watershed, site and section scales have been tested by permuting whole sections, permuting sections within watersheds and permuting sections within sites, respectively. The second type of null models followed an environmentally, a spatially and, an environmentally and spatially constrained version. In this case, the likelihood of species co-occurrences were assessed once species environment affinities and-or continuous spatial structure have been factored out as a possible explanation for the observed patterns detected by the unconstrained version (Peres-Neto et al., 2001). Species distributions were modelled using environmental and/or continuous spatial descriptors (*i.e.,* eigenvector maps), accordingly, and the probabilities of occurrence were used as the likelihood of species occupying particular sites during the generation of null communities. The probabilities were estimated by a discriminant function, where each species presence/absence were analysed by a selection of explanatory variables (environmental and-or spatial). Finally, null models (*e.g.,* environmentally constrained version, spatially constrained version and, environmentally and spatially constrained version) were contrasted to assess the likelihood that environmental and continuous spatial descriptors influenced patterns in species pairwise co-occurrences (tabl. 2.9). This analysis was performed in Matlab and tested using 999 permutations.

2.2.4.7 Hierarchical diversity partitioning across nested spatial scales: watershed, site and section

Diversity patterns can also provide additional information concerning species distributions and community structure. The landscape diversity can be partitioned into additive components associated to different hierarchical levels, such as spatial or temporal scales. Compared to the previous analyses, this partitioning respects the hierarchical nature of the landscape and estimates the variability in species distributions present at a level, while accounting for the variability associated to the levels below. For instance, the variability in species composition among sections within sites is obtained from this analysis, as opposed to the landscape variability across all sections as in early analyses (tabl. 2.4). We partitioned compositional differences among spatial units using the approach of Veech and Crist 2007; results are presented in table 2.10). This analysis was performed in Matlab and tested by 999 permutations.

2.3 Results

Out of seventeen species, ten presented significant preferences for riffles, runs or pools (tabl. 2.3). The species displaying habitat selection were the pumpkinseed sunfish and the brown bullhead that significantly preferred pools and avoided riffles. Rock bass and the central mudminnow avoided riffles. Cut lips and logperch selected runs and avoided pools. Brook trout and longnose dace preferred riffles and avoided pools. The white sucker and fallfish were found in runs and avoided riffles.

The variation associated with the distribution of each species, the community and the environment were partitioned among the nested spatial scales namely, watershed, site and section (tabl. 2.4). The variation associated exclusively to watershed scale ([a]) is zero, indicating that there is no difference in environment and in species composition (*i.e.,* beta diversity) across watersheds. Negative values are due to fraction adjustment. All species present variability at the site scale ([c]), varying between 21% for brown bullhead to 74% for brook trout. When all species were considered together (*i.e.,* community), the variability across sites was 52%. The variability of the environment across sites corresponded to 37% and was significant. Thus, at the site scale, species distributions were more variable than environmental conditions. The watershed and site shared some variation ([b]). For single species distribution, this fraction varied from 0 to 14%, being 5% for the community and 4% for the environment. The residual fraction ([d]) corresponded to the variability present at section scale (*i.e.,* differences among sections independent of site and watershed differences). For single species distribution, this fraction varied from 25% for brook trout to 71% for brown bullhead. The section scale represented 44% of the variation for all species combined (*i.e.,* community). In the case of the environment, 61% of the variability was linked to the section scale. Overall, species distributions were more variable across sites, while environmental variability was greater at the section scale.

Table 2.3

Results of the chi-square analyses evaluating species habitat selection. Species common name, percentages of used habitat (*e.g.*, %Riffle), chi-square statistic and associated probability are presented, significant probabilities are shown in bold and, significant habitat preferences are indicated by (+), whereas avoidances are indicated by (-)

Species name	% Riffle	% Run	% Pool	Chi-square	Prob
Creek chub	0.28	0.37	0.35	2.39	0.3023
Pumpkinseed sunfish	0.20 (-)	0.35	0.45 (+)	10.39	**0.0055**
Common shiner	0.30	0.41	0.29	2.90	0.2337
Rock bass	0.18 (-)	0.41	0.41	9.83	**0.0073**
Cut lips	0.32	0.45 (+)	0.23 (-)	7.67	**0.0215**
Brook trout	0.53 (+)	0.27	0.20 (-)	10.97	**0.0041**
Central mudminnow	0.12 (-)	0.43	0.45	9.52	**0.0085**
White sucker	0.16 (-)	0.46 (+)	0.38	7.11	**0.0285**
Brown bullhead	0.20 (-)	0.24	0.56 (+)	10.19	**0.0061**
Yellow perch	0.25	0.40	0.35	1.13	0.5663
Smallmouth bass	0.38	0.42	0.20	2.93	0.2300
Fallfish	0.05 (-)	0.69 (+)	0.26	18.85	**0.0001**
Longnose dace	0.61 (+)	0.34	0.05 (-)	11.78	**0.0028**
Fathead minnow	0.21	0.52	0.27	3.16	0.2057
Pearl dace	0.44	0.23	0.33	0.99	0.6091
Logperch	0.20	0.80 (+)	0.00 (-)	6.06	**0.0482**
Brown trout	0.48	0.22	0.30	0.90	0.6367

Table 2.4

Results of the variation partitioning of species distribution and environmental variability across nested spatial scales (*e.g.*, watershed, site and section). These analyses were conducted at the species, community and environment levels, the adjusted-R^2 (Adj. R^2) of different fractions and probabilities are indicated for each scale and, significant probabilities are shown in bold

	Watershed		Shared	Site		Section
	Adj. R2 [a]	Prob [a]	Adj. R2 [b]	Adj. R2 [c]	Prob [c]	[d]
Creek chub	-0.01	0.51	0.03	0.59	**0.0101**	0.39
Pumpkinseed sunfish	-0.01	1.00	0.03	0.43	**0.0101**	0.55
Common shiner	-0.01	**0.01**	0.12	0.55	**0.0101**	0.34
Rock bass	-0.01	**0.01**	0.04	0.67	**0.0101**	0.30
Cut lips	-0.01	1.00	0.02	0.67	**0.0101**	0.32
Brook trout	-0.01	1.00	0.01	0.74	**0.0101**	0.25
Central mudminnow	-0.01	1.00	-0.01	0.55	**0.0101**	0.46
White sucker	-0.01	0.76	0.06	0.28	**0.0101**	0.67
Brown bullhead	-0.01	**0.01**	0.10	0.21	**0.0101**	0.71
Yellow perch	-0.01	**0.01**	0.03	0.42	**0.0101**	0.56
Smallmouth bass	-0.01	**0.01**	0.01	0.60	**0.0101**	0.40
Fallfish	-0.01	**0.01**	0.13	0.46	**0.0101**	0.41
Longnose dace	-0.01	**0.01**	0.01	0.49	**0.0101**	0.51
Fathead minnow	-0.01	0.95	-0.01	0.54	**0.0101**	0.47
Pearl dace	-0.01	**0.01**	0.03	0.65	**0.0101**	0.32
Logperch	-0.01	**0.01**	0.14	0.34	**0.0101**	0.53
Brown trout	-0.01	1.00	0.03	0.51	**0.0101**	0.47
Community	-0.01	**0.01**	0.05	0.52	**0.0101**	0.44
Environment	-0.01	**0.01**	0.04	0.37	**0.0101**	0.61

Thirteen environmental variables were selected, accounting for 21% of the species distributions (tabl. 2.5). Those variables were used in further analyses to represent the environmental conditions linked to species distributions.

Only the distance biplot was presented since both scaling, namely distance and correlation biplots, were very similar. Thus, we can interpret the correlations among all variables from both sets as well. The first two axes were both significant ($p = 0.0010$) and together accounted for 16.17 % of the variation in species distributions across sections. Species seemed to cluster in part according to family and in part to ecological similarities (fig. 2.3). The centrarchidae (rock bass, pumpkinseed sunfish and smallmouth bass) and yellow perch appeared clustered in the biplot where they were associated to deeper, wider and warmer habitats (*i.e.,* sections) with smoother stream slopes. Many cyprinidae (cut lips, fallfish and fathead minnow) as well as logperch were found in warmer and wider streams with sharp bank slopes. Longnose dace was isolated in the biplot, with a preference for habitats containing riffles, cobble substrate, no silt, dense vegetation and sharp bank slopes. The two salmonidae (brown trout and brook trout) and pearl dace selected habitats with cool, shallow water, mostly riffle with no macrophytes, no pebble and sharp stream slopes. Three benthic species (white sucker, central mudminnow and brown bullhead), common shiner and creek chub avoided riffle habitats and their presence was associated with habitats containing silt, pebble, macrophyte, no cobble and a light bank vegetation.

Table 2.5
Environmental variables that were significantly related to species distribution. Adjusted cumulative R^2 (Adj. R^2 Cum.), F values and probability are presented for each variable and, significant probabilities are shown in bold

Environmental variables	Adj. R2 Cum.	F value	F Prob
Water temperature	0.07	11.19	**0.0010**
Riffle habitat	0.09	4.31	**0.0010**
Width average	0.11	3.56	**0.0010**
Depth average	0.12	3.40	**0.0010**
Slope of the bank	0.13	2.91	**0.0020**
Vegetation of the bank	0.14	2.97	**0.0030**
Slope of the stream	0.16	2.87	**0.0030**
Length of the section	0.17	2.71	**0.0040**
Industrial or commercial zone	0.18	2.70	**0.0040**
Cobble percentage	0.19	2.45	**0.0070**
Silt percentage	0.20	2.62	**0.0040**
Macrophyte percentage	0.20	2.31	**0.0090**
Pebble percentage	0.21	2.02	**0.0230**

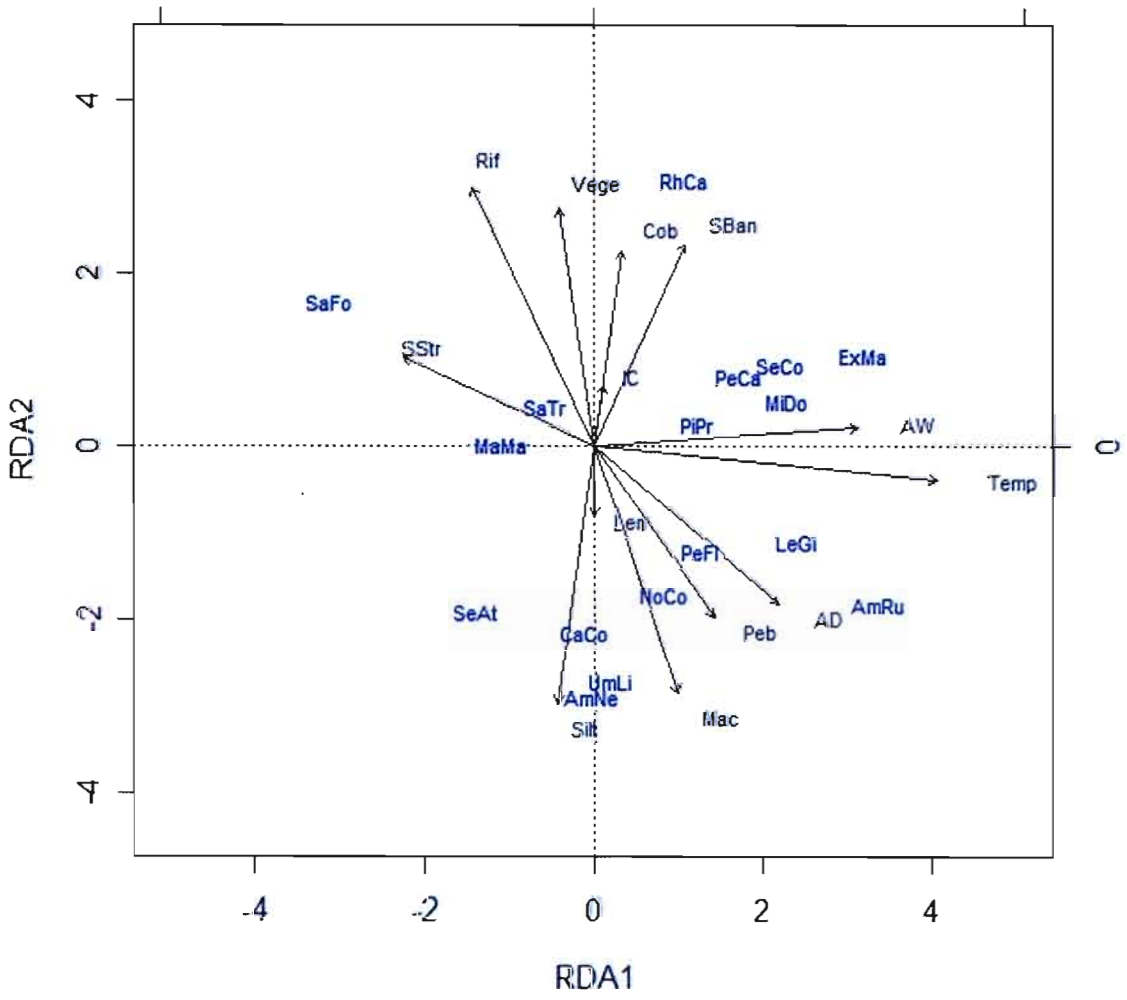


Figure 2.3 RDA distance biplot showing the relationship between species distributions and selected significant environmental variables (see tabl. 5 for variables and probabilities), both represented by their code (see tabl. 1 and tabl. 2 for variables and species codes, respectively). The first two axes were significant ($p = 0.0010$) and accounted for 16.17 % of species distributions.

After partitioning species distribution and environmental variability across nested spatial scales (tabl. 2.4), the variability in species distribution which is explained by the environment was further partitioned among nested spatial scales for each species and for the whole community (tabl. 2.6). At the site scale, the environment explained significantly 31% of community distribution ([a]). This fraction varied between 57% for brook trout down to 6% for brown trout and was significant for eight species. Since the variability present at the watershed scale was 0, the fraction ([c]) was associated to the section scale and there was almost no variability explained by the environment (maximum of 4% for the central mudminnow). The fraction ([b]), shared by the different scales, was trivial. Even thought part of the variation in species distributions was linked to the environment at the site scale, a large fraction (residual [d]) remained unexplained.

The water course distance among sites that provided the best representation of the continuous spatial structure of the system network, was assessed for single species distribution, community and environment, with the continuous spatial descriptors (*i.e.,* representing positively autocorrelated variation) computed from total, upstream and downstream distance. Overall, for both species distributions and environmental conditions, total distance exclusively explained the largest fraction of the variability, respectively 6% and 11% (tabl. 2.7).

The selected environmental variables (tabl. 2.5) and the continuous spatial descriptors (*i.e.,* eigenvector maps) computed from the total distance among sites (tabl. 2.7) uniquely explained 21% and 8% of species distribution variability, respectively, and both fractions were highly significant ($p = 0.0010$) (fig. 2.4). The shared fraction ([b]) was quite small representing only 3% of the variation (fig. 2.4). Thus, the response of species distributions to environmental variables was not strongly spatially structured.

Table 2.6

Variation partitioning of single species and community distribution variability that are explained by the selected environmental variables (tabl. 5) between site and section scales and, significant probabilities are shown in bold

	Site		Shared	Section		Residual
	Adj. R2 [a]	Prob [a]	Adj. R2 [b]	Adj. R2 [c]	Prob [c]	[d]
Creek chub	0.42	**0.0090**	-0.04	0.01	**0.0060**	0.61
Pumpkinseed sunfish	0.20	0.2543	-0.01	-0.04	0.6096	0.85
Common shiner	0.34	0.0761	-0.03	-0.02	0.0771	0.70
Rock bass	0.38	0.0691	-0.03	-0.03	0.2382	0.68
Cut lips	0.37	0.0541	-0.03	0.01	**0.0010**	0.65
Brook trout	0.57	**0.0040**	-0.05	-0.01	**0.0080**	0.48
Central mudminnow	0.42	**0.0020**	-0.04	0.04	**0.0020**	0.58
White sucker	0.25	**0.0210**	-0.02	-0.02	0.4024	0.79
Brown bullhead	0.25	**0.0110**	-0.02	-0.02	0.5215	0.79
Yellow perch	0.15	0.3423	-0.01	-0.04	0.2282	0.90
Smallmouth bass	0.14	0.6256	-0.01	-0.04	0.5425	0.92
Fallfish	0.37	**0.0120**	-0.03	-0.01	0.2442	0.67
Longnose dace	0.31	**0.0260**	-0.03	0.02	**0.0050**	0.70
Fathead minnow	0.02	0.9510	0.00	-0.04	0.2272	1.01
Pearl dace	0.24	0.3964	-0.01	-0.04	0.2012	0.81
Logperch	0.15	0.3153	-0.00	-0.06	0.6607	0.91
Brown trout	0.05	0.9028	0.00	-0.08	0.8108	1.02
Community	0.31	**0.0010**	-0.02	-0.02	**0.0010**	0.73

Table 2.7

Comparison of continuous spatial descriptors (*e.g.,* eigenvector maps) computed from total, upstream and downstream water course distances among sites. Adj. R^2 of the fractions and probabilities are indicated for single species distribution, community and environment as well as for each distance and, significant probabilities are shown in bold

	Total distance [a]		Upstream distance [b]		Downstream distance [c]		Residuals
	Adj. R2 [a]	Prob [a]	Adj. R2 [b]	Prob. [b]	Adj. R2 [c]	Prob [c]	[h]
Creek chub	0.10	**0.0070**	0.01	0.1780	0.11	**0.0010**	0.77
Pumpkinseed sunfish	0.03	0.1160	0.02	0.1580	0.08	**0.0110**	0.74
Common shiner	0.03	0.1220	0.03	**0.0440**	0.20	**0.0010**	0.72
Rock bass	0.08	**0.0100**	0.03	0.1020	0.15	**0.0010**	0.71
Cut lips	0.28	**0.0010**	0.18	**0.0010**	0.12	**0.0010**	0.55
Brook trout	0.12	**0.0020**	0.08	**0.0050**	0.13	**0.0010**	0.69
Central mudminnow	0.08	**0.0130**	0.08	**0.0050**	0.12	**0.0020**	0.77
White sucker	0.17	**0.0010**	0.02	0.1940	0.05	**0.0435**	0.77
Brown bullhead	0.07	**0.0230**	-0.01	0.7800	0.01	0.2820	0.85
Yellow perch	0.25	**0.0010**	0.11	**0.0020**	0.13	**0.0020**	0.70
Smallmouth bass	0.09	**0.0140**	0.066	**0.0180**	0.06	**0.0280**	0.80
Fallfish	0.13	**0.0020**	0.02	0.1240	0.00	0.3980	0.76
Longnose dace	0.13	**0.0010**	0.05	**0.0310**	0.01	0.3120	0.71
Fathead minnow	0.01	0.3730	0.11	**0.0020**	0.03	0.1130	0.84
Pearl dace	0.05	0.0990	0.03	0.1410	0.06	**0.0400**	0.92
Logperch	0.35	**0.0010**	0.21	**0.0010**	0.11	**0.0010**	0.50
Brown trout	0.15	**0.0050**	0.06	**0.0250**	0.01	**0.0321**	0.85
Community	0.11	**0.0010**	0.06	**0.0010**	0.09	**0.0010**	0.74
Environment	0.06	**0.0010**	0.05	**0.0010**	0.04	**0.0010**	0.85

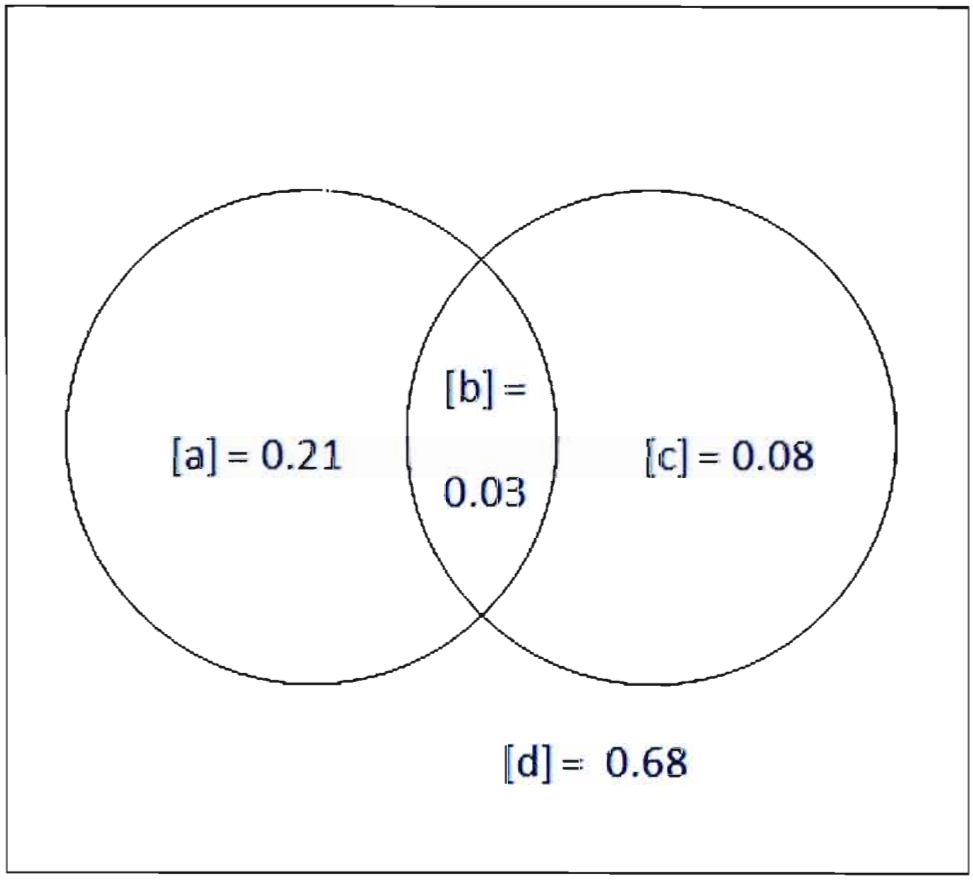


Figure 2.4 Venn diagram representing the variation partitioning of species distributions variability between the selected environmental variables (tabl. 2.5) [a] and the continuous spatial descriptors computed from the total distance among sites (tabl. 2.7) [c] and, the two fractions are highly significant (p = 0.0010).

A stepwise forward selection was conducted to retain eigenvectors computed from the total distance among sites that were significantly related to species distributions (tabl. 2.8). Moran's I, representing the spatial autocorrelation associated to each eigenvector, is a measure of the continuous spatial scale. The first eigenvector represented large scale patterns and were associated with the greatest Moran's I, while the last ones were linked to smaller scales. The seven first eigenvectors (out of 13) were significant and accounted for 11% of the variability is species distributions (*i.e.*, beta diversity).

Table 2.8

Eigenvectors computed from the total distance among sites significantly related to species distribution, Moran's *I* measuring the extent of the associated spatial autocorrelation, Adj. R^2 Cum., F-statistic and associated probabilities are presented for each significant eigenvectors and, significant probabilities are outlined in bold

Eigenvector	Moran's I	Adj. R2 Cum.	F	Prob
2	0.3892	0.03	5.43	**0.0010**
1	0.8568	0.05	3.58	**0.0010**
7	0.0143	0.06	3.47	**0.0020**
3	0.0797	0.08	3.20	**0.0010**
6	0.0043	0.09	3.11	**0.0010**
5	0.0043	0.10	2.84	**0.0030**
4	0.0636	0.11	2.19	**0.0200**

Different species co-occurrence patterns have been observed across different nested spatial scales and appear to be linked to environmental and spatial factors (*e.g.*, eigenvector maps) (tabl. 2.9). The unconstrained null models based on the C-score (*i.e.*, joint absence) were significant at the site and watershed scales and the T-score (*i.e.*, joint presence) at all nested scales. The environmentally constrained model showed significant C-scores only at the watershed scale and significant T-score at all nested scales. By contrasting the unconstrained model against the environmentally constrained model, species habitat requirements appeared responsible for the patterns in species negative co-occurrence at the site scale. However, significant patterns remained after controlling for the environment. The continuously spatially constrained null model using the eigenvectors computed from the total and downstream distance suggested significant C- and T-score for the site scale, and for the downstream distance significant T-score at the section scale. By contrasting the unconstrained model against the continuously spatially constrained model, continuous spatial structure appear to be linked to species co-occurrence patterns at the watershed scale. When environmental and continuous spatial constraints were jointly imposed to the null model, the global C-score was no-longer significant, global T-score was significant at the section scale and for the total distance at the site scale. Species negative co-occurrences were explained by species environmental affinities and continuous spatial structure, while parts of species positive co-occurrences remained at the small scales after controlling for those factors. The model using total distance suggested that at the scale section, creek chub appeared to be positively associated with common shiner, yellow perch and pearl dace, the pumpkinseed sunfish appeared to be positively associated with rock bass, cut lips, smallmouth bass and fathead minnow, rock bass with smallmouth bass, central mudminnow with yellow perch and pearl dace, yellow perch with brown trout and finally, smallmouth bass and fathead minnow. At the site scale, creek chub appeared positively associated with cut lips and yellow perch, pumpkinseed sunfish with common shiner, rock bass, yellow perch and smallmouth bass, common shiner with cut lips, central mudminnow, yellow perch, and longnose dace, rock bass with cut lips, brown bullhead, smallmouth bass, fallfish and logperch, cut lips with fallfish, longnose dace and logperch, central mudminnow with yellow perch and smallmouth bass, the brown bullhead with smallmouth bass, yellow perch with brown trout, smallmouth bass with longnose dace and logperch and finally, logperch with fallfish and fathead minnow.

Table 2.9

Null model results. C-score and T-score global probabilities across nested spatial scales for unconstrained, environmentally constrained, spatially constrained (*e.g.*, eigenvector maps), and environmentally and spatially constrained models are presented and, significant probabilities are in bold

	Watershed	Site	Section
Unconstrained			
Prob C-score	**0.0010**	**0.0010**	0.6096
Prob T-score	**0.0010**	**0.0010**	**0.0030**
Environmentally Constrained			
Prob C-score	**0.0080**	0.0751	0.5265
Prob T-score	**0.0020**	**0.0320**	**0.0290**
Spatially Constrained			
Eigenvectors-Total distance			
Prob C-score	0.9950	**0.0310**	0.3974
Prob T-score	1.0000	**0.0010**	0.1111
Eigenvectors-Downstream distance			
Prob C-score	0.3083	**0.0040**	0.7538
Prob T-score	0.3073	**0.0010**	**0.0110**
Environmentally and spatially Constrained			
Eigenvectors-Total distance			
Prob C-score	0.7768	0.2262	0.5816
Prob T-score	0.9870	**0.0050**	**0.0120**
Eigenvectors-Downstream distance			
Prob C-score	0.3664	0.6677	0.4735
Prob T-score	0.8529	0.2472	**0.0460**

Regarding the hierarchical partitioning of diversity across nested spatial scales, most of the variation was found at the medium scale (*i.e.*, across sites within watersheds) rather than at the large (*i.e.*, across watersheds within the landscape) and small (*i.e.*, across sections within sites) scales. On average, watersheds differed by 1.67 species, representing 13.37% of the beta diversity component, sites differed on average by 8.39 species or 67.26% of the beta diversity and sections differed by 2.42 species or 19.38% of the beta diversity (tabl. 2.10). The beta diversity were significant for the watershed and site scale but not at the section scale. Note however, that although the section component was larger than the watershed components, the former was not significant since only between 3 to 5 sections were sampled per site, which reduced the power of detecting a significant value. These results are in contrast with the ones based on a non-hierarchical analysis using variation partitioning (tabl. 2.4). The exclusive fractions of the non-hierarchical version suggested that there was no variation in species composition at the watershed scale, a large variation across sites (52%) and sections (44%). In the hierarchical version only the variation across sections within sites and across sites within watersheds are considered, whereas the non-hierarchical version (tabl. 2.4) assessed the variation across all sections independent of sites and watersheds.

Table 2.10

Partitioning of the total diversity according to the nested spatial scales (*e.g.,* watershed, site and section), total γ species diversity corresponds to the 17 species present in the landscape, components of α and β diversity, relative contribution (% beta) and probability of β diversity are presented and, significant probabilities are in bold

	Watershed	Site	Section
Alpha	15.33	6.94	4.53
Beta	1.67	8.39	2.42
(%) Beta	13.37	67.26	19.38
Prob Beta	**0.0010**	**0.0010**	1.0000

2.4 Discussion

Defining the relevance of spatial scales in structuring species distributions, co-occurrence and diversity patterns as well as their relationships with the environment may improve our understanding of ecological processes. In streams located in the Laurentian region, Québec, Canada, different biological descriptors were evaluated for 17 species and compared across 3 spatial scales (*e.g.,* watershed, site and section). Although the proportion of variation explained by environmental features at different spatial scales has been previously assessed (Deschênes and Rodríguez, 2007; Reyjol et al., 2008), the comparisons of many species and biological descriptors remain necessary. These contrasts can identify the scales at which different patterns can be best detected for a given species and can therefore guide the choice of environmental features and measurement grain required for particular cases.

2.4.1 Habitat selection

When species distributions across different mesohabitats (*e.g.,* riffle, run and pool) were compared at the section scale, we found that 60% of the community selected or avoided particular mesohabitats. Riffles were avoided by central mudminnow, white sucker, brown bullhead, pumpkinseed sunfish, rock bass and fall fish, perhaps because this mesohabitat has high turbulent flow (Hynes, 1970; Allan, 1995). Negative effects of high flow on stream fish abundance have been reported (Freeman et al., 2001; Roghair et al., 2002). Central mudminnow, white sucker and brown bullhead are known to have a benthic behaviour (Bernatchez and Giroux, 2000), which suggests that they are poor swimmer at high currents. Brook trout preferred riffles and avoided pools and this species has a preference for cooler and highly oxygenated water (Bernatchez and Giroux, 2000), which is the type of habitat present in riffles (Hynes, 1970; Allan, 1995). Species of different families such as cyprinidae (*e.g.,* creek chub, common shiner, fathead minnow, and pearl dace), centrarchidae (*e.g.,* smallmouth bass), percidae (*e.g.,* yellow perch) and salmonidae (*e.g.,* brown trout) were indifferent to these habitat types.

2.4.2 Species distribution and environmental variability and relationship across nested spatial scales

Whenever ecologists adopt a multi-scale or hierarchical perspective in their research, variance partitioning can be a powerful tool to explicitly account for the nested structure in statistical analyses and decompose the variability across scales. At the **smallest scale**, around 35 meters, fish did not respond to the environmental variability present, even if sections were the most variable in their environmental conditions. It is possible that fish need larger areas than what is available in the sections considered here to accomplish their daily activities and complete their life history cycles, such as resting, feeding, mating and avoiding predation. Although stream fish movements are known to be spatially limited for some species (Gatz and Adams, 1994; Skalski and Gilliam, 2000; Schaefer, 2001, Roberts and Angermeier 2007), it seemed that the section scale was smaller than the area used by riverine fish for their daily activities. Moreover, the presence of local adaptations to environmental conditions present at this scale (see chapter 2) may explain why there was no relationship between species distributions and environmental conditions at this scale (McPherson and Jetz, 2007). Environment was most influential at **intermediate scale**. The largest variation in composition and response to environment occurred at the site scale, representing reaches of 130 meters in average. Mesohabitat types (*e.g.,* riffle, run and pool) as well as water temperature, stream and bank slopes, section width, depth and substrate composition were the most important in explaining species distributions, though a large fraction of their variation remained unexplained. The sampling date did not appear to influence species distribution, suggesting that species response to variables do not vary through time. Although, we are fairly confident that species presence-absence reflected appropriately the community present, a more exhaustive sampling through time could have improved statistical power and perhaps improve our knowledge about the system (Roberts and Angermeier, 2007), such as community stability, species daily movement and dispersal capacity. At the **largest scale** considered, little variability among watersheds in terms of species and environment was observed. Similarly, a study on brook trout in the Cascapedia River basin, Canada, found that variation in density at the largest scale (*e.g.,* among streams of different watersheds) was small relatively to the smaller scales (*e.g.,* among reaches and sections) (Deschesnes and Rodríguez, 2007). Another study that looked at community assemblage, suggested that there

is less variation among than within tributaries (Reyjol et al., 2008). Large scale variation in riverine community may be present but at a scale larger than adjacent watersheds, such as among different geological regions or countries. For instance, differences in coral fish assemblage have been reported across the Indio-Pacific (Belmaker et al., 2008).

The variation in species distributions explained by the environment at the site scale varied across species from 57% for the brook trout to 2% for the fathead minnow. Many factors may explain this variation in predictive power, such as association with poorly sampled habitats, species body size, habitat tolerance and distinctiveness, dispersal and movement behaviour, range size, rarity, response to conspecifics and trophic level (McPherson and Jetz, 2007). Especially, polymorphism is known to be common among freshwater fish (Robinson and Parsons, 2002) and may also contribute to explain variation across species (see Chapter 2). Indeed, an important underlying assumption of species modeling frameworks is that species are essentially the same entity throughout their range. For species that have the potential for physiological and morphological plasticity and hence local adaptation, this assumption may be invalid. For example, if an insect living in a warmer climate grows a thicker cuticle, a fish living in colder water grows more gill lammellae, or a damselfly that has to commute further from stream to forest grows longer wings (Taylor and Merriam, 1995), members of a resident population may be able to survive in areas that would be inaccessible to adult members of the same species elsewhere in its range. Habitat modelling may therefore provide an inaccurate picture of what constitutes a suitable habitat for polymorphic species. This potential weakness is particularly true for models based on presence-absence data, which often indicate a far greater potential range than the realized range.

2.4.3 Continuous spatial predictors: eigenvectors maps

The best model for the continuous spatial structure (*i.e.*, eigenvector maps) of the stream network was produced by predictors based on the total water course distance, and it was not strongly associated to the environment but was linked to species distributions and patterns of co-occurrence. The non-directional total distance may have encompassed the directional upstream and downstream variability. Species distributions appeared to be influenced mostly by large scale processes since eigenvectors smaller than the seventh one were not significant. Continuous spatial descriptors may represent contagious spatially structured processes such as connectivity, isolation, dispersal, local adaptation and unmeasured spatially structured variables (Borcard and Legendre, 2002; Dray et al., 2006; Griffith and Peres-Neto, 2006). Integrating spatial descriptors into models usually improves their performance but may also bring some disadvantages when attempting to use the model in other landscapes (*i.e.*, validation). For instance, it has been shown that models that incorporate a spatial autocorrelation term, reflecting environmental rather than biological spatial structure, will hardly be applicable to other situations across space, because the spatial arrangement of environmental gradients may differ (Guisan and Thuiller, 2005). However, a positive side is that we can consider model estimates for the environmental component of the model alone (*i.e.*, independent of space). In this case, model performance in other landscapes may increase as the dependence of spatial arrangement is removed, increasing model portability (*i.e.*, application in other landscapes; Maggini et al., 2006).

2.4.4 Co-occurrences patterns across nested spatial scales

Species co-occurrence can be the result of biotic, spatial and environmental processes (or a combination of these factors; Stone and Roberts, 1992; Peres-Neto et al., 2001; Peres-Neto, 2004; Sfenthourakis et al., 2005). By contrasting unconstrained, environmentally constrained, spatially constrained and, environmentally and spatially constrained null models, we were able to evaluate whether environmental preferences and spatial processes or biotic interactions were most important in shaping patterns in species co-occurrences. The unconstrained model showed negative species co-occurrence at the site and watershed scales,

and positive associations at all scales. Species environmental preferences seemed responsible for negative co-occurrence at the site and section scales. This contrast was anticipated by Peres-Neto et al. (2001), who rationalized that environmental relationships can drive species to occur in similar or different habitats, inducing, respectively, positive or negative patterns in species co-occurrences. Patterns in species co-occurrence were mostly influenced by the continuous spatial descriptors at the site and watershed scales. Although we did not consider the spatial variation within sites, smaller scale variations did not seem to affect our spatial model. The co-occurrence patterns explained by the spatial descriptors may be the product of dispersal, isolation, local adaptation and unmeasured spatially structured variables (Borcard and Legendre, 2002; Dray et al., 2006; Griffith and Peres-Neto, 2006). Once environment and the continuous spatial structure were accounted for, species positive co-occurrences were still present at small scales (*e.g.,* site and section), suggesting true biotic interactions, such as facilitation or predation. These results are consistent with other studies, which have suggested that at broad extents and coarse resolutions, facilitation and competition should have smaller effects on community structure than at more local extents and finer resolution (Huston, 2002; Pearson and Dawson, 2003), though cases of facilitation in fish are not well recorded. Nevertheless, we observed positive associations across a wide range of species and family (*e.g.,* cyprinidae, centrarchidae, salmonidae, umbridae, ictaluridae and percidae). The species that did not seem to interact positively at any scale were white sucker and brook trout. Perhaps the wide range of conditions tolerated by white sucker and the generalist diet of brook trout (Bernatchez and Giroux, 2000), make them less prone to biotic interactions.

2.4.5 Diversity partitioning across spatial scales

The partitioning of the total diversity of the entire studied area into additive components according to the hierarchical nature of the sampling design (*e.g.,* wathershed, site and section) was useful in evaluating the levels of variability in species distributions present at a scale, while accounting for the variability associated to the other scales (Lande, 1996; Pélissier and Couteron, 2007; Veech and Crist, 2007; Belmaker et al., 2008). As opposed to the non-hierarchical approach (tabl. 2.4), it provided different variability estimates associated to each scale. The contrast between both approaches (hierarchical *versus* non-hierarchical) is often

not considered even though it can change our perception of the importance of scales and the associated processes driving community structure. Indeed, when the hierarchical structure was accounted for, it lessened the species distributions variability associated to the section scale, and increased the variability at the watershed and site scales, in contrast to the non-hierarchical scheme (contrast tabl. 2.4 and tabl. 2.10). The contrasts between the hierarchical and non-hierarchical approaches may be linked to processes that take place at different scales. Given that fish are fairly restricted in their daily movements, they may have to explore an entire site to choose a specific section (*e.g.,* mesohabitat), but will hardly visit many sites in their life span (Roberts and Angermeier, 2007). The hierarchical approach, which estimates the variability across sections within sites (Lande, 1996; Pélissier and Couteron, 2007; Veech and Crist, 2007), may be better suited to assess the short term variability encountered by fish. However, if long-term processes such as local and regional colonization-extinction dynamics or evolution of specific adaptations are the processes of interest, the non-hierarchical approach may be more appropriate to quantify the variability among all sections, sites or watersheds across a specific landscape. Here, given the greater temporal and spatial scales required for these processes to occur, the non-hierarchical approach may be more adapted to address those issues. Therefore, the differences between the two approaches are not analytical but conceptual, and each one should be used in the appropriate context in order to improve our understanding of community structure.

2.4.6 Conclusion

Although nested designs have been previously used to account for spatial structure of stream systems (Deschênes and Rodríguez, 2007; Reyjol et al., 2008), their potential to enhance our understanding of biological patterns across spatial scales and species still remains largely unexplored. By applying a nested sampling design and using information available at different spatial scales, the nested analyses allowed the identification of the relevant spatial scales and their importance in structuring different aspects of these riverine fish assemblages. Even though the spatial scales investigated in this study may not have been ideally designed to fit species particularities at small and large scales, the statistical framework was helpful in determining meaningful scales, describe multi-species distributions, co-occurrence and

diversity patterns across spatial scales. This study supports the notion that there is no best scale at which to examine biological patterns and outlined the necessity to consider several scales to understand a system (Burke and Grime, 1996; Tilman, 1997; Connolly and Roughgarden, 1998; Thuiller et al., 2003). Perhaps, the issues revolving spatial scales may be responsible for many ecological debates and theoretical disagreements in the literature. Indeed, the use of different geographical extents might provide unequivocal answers to the same question. Given that species assemblages are structured by factors that operate across multiple spatial scales, an understanding of these species-environment relationships through space are crucial to provide information to help manage, conserve and restore biodiversity. For instance, the appropriate scale of conservation is likely dependant on dispersal ability of organisms, thus section or site scale management may only be appropriate for low dispersers, while watershed scale protection may be needed for organisms with high levels of dispersion. Identifying the scales at which species respond to habitat characteristics allows managers to apply management and conservation efforts at the appropriate level.

SECOND CHAPITRE

HOW DO ENVIRONMENTAL CONDITIONS TRIGGER PHENOTYPIC VARIABILITY? MORPHOLOGICAL AND SWIMMING CAPACITY PATTERNS OF DIFFERENTIATION AMONG HABITAT TYPES OF RIVERINE FISH

Comment les conditions environnementales affectent la variabilité phénotypique? Les patrons de différentiation morphologique et de capacité de nage entre les mésohabitats des poissons en rivière

ABSTRACT

Polymorphism is an ecological strategy that allows populations from a single species to partition resources through variation of functional traits adapted to their respective habitats. Stream fish may experience great spatial variation in their habitat, which may have important developmental consequences and/or act as a selective pressure in driving phenotypic variation. Here, we assess whether contrasting stream mesohabitats (*e.g.*, riffle, run and pool) can lead to species polymorphism and population differentiation regarding morphology and swimming capacity. The specific objectives are as follows: (1) Assess and determine morphological variation within and between species across stream mesohabitat types and their relationship with environmental descriptors; (2) Compare phenotypic integration (*i.e.*, correlations among traits) within species across mesohabitat types and (3) Evaluate the relationship between habitat use, morphology and swimming capacity. Our results indicate that morphological differences existed across species and that 80% of the species were polymorphic in regards to habitat, though patterns were not consistent across species. Moreover, environmental variables were related to morphological characteristics for all species. Levels of phenotypic integration among habitat types did not differ and no relationship between habitat use, morphology and swimming capacity was found.

Keywords: distribution, environment, fish, geomorphometrics, multi-species, polymorphism, stream, swimming capacity.

La relation entre l'environnement et la variabilité phénotypique de la morphologie et de la capacité de nage de 10 espèces de poissons des rivières a été évaluée. Des patrons de différentiation morphologique ont été retrouvés entre les types d'habitat pour 80% des espèces. Ces variations morphologiques sont présentes entre les populations provenant de différents mésohabitats indépendamment des bassins versants, mais ne sont pas constantes entre les espèces. Il est possible que différentes espèces aient des stratégies particulières pour surmonter des défis semblables. Les espèces qui n'ont pas démontré de divergences sont benthiques, ce qui peut expliquer qu'ils ressentent et répondent moins aux caractéristiques environnementales. Le mésohabitat ne semble pas affecter le niveau d'intégration phénotypique des populations, bien qu'il semble y avoir des différences entre les espèces. Aucune relation significative n'a été observée entre la capacité de nage et le type d'habitat, l'identité des espèces, les descripteurs reflétant la distribution ou la sélection d'habitat et la morphologie. La mesure de capacité de nage utilisée ne semble pas représenter adéquatement les défis écologiques et physiologiques auxquels font face les poissons des rivières.

Mots clés: capacité de nage, distribution, environnement, géomorphométrie, multi-espèce, poisson, polymorphisme, rivière.

CHAPITRE II

HOW DO ENVIRONMENTAL CONDITIONS TRIGGER PHENOTYPIC VARIABILITY? MORPHOLOGICAL AND SWIMMING CAPACITY PATTERNS OF DIFFERENTIATION AMONG HABITAT TYPES OF RIVERINE FISH

3.1 Introduction

3.1.1 Variation in fish morphology and swimming capacity across habitats

Polymorphism is an ecological strategy that allows populations from a single species to partition resources through variation of specific functional traits adapted to their respective habitats, such as phenotypic variation in morphological, behavioral, life-history or physiological characteristics. Phenotypic variations among groups of individuals can be associated to genetic and/or plasticity (*e.g.,* influence of the environment on the phenotype) (West-Eberhard, 1989; Price et al., 2003). Functional traits relate to resource use and habitat requirements and may contribute to turnover in species composition (Wellborn et al., 1996; Stoks and McPeek, 2003; Jacquemyn et al., 2005; Leclerc and DesGranges, 2005), help understand the processes that drive co-occurrence patterns (Armbruster et al., 1994; Silvertown, 2004; Stubbs and Wilson, 2004) and have the potential to elucidate the processes driving population and species differentiation (McIntyre et al., 1999; Lavorel and Garnier, 2002; Wright et al., 2005). Phenotypic variation is considered common among vertebrates (Skúlason and Smith, 1995), but is especially pronounced In fish populations (Snorrason et

al., 1994; Skúlason and Smith, 1995; Bourke et al., 1997). Indeed, fish are recognized to be flexible in regards to many life-history characteristics that are capable of quickly adapt to environmental conditions (Snorrason et al., 1994). Because of the high density of the surrounding medium present in aquatic system, morphological variation in fish should be pronounced (Webb, 1984). Because morphological characteristics may constrain fish abilities to utilize particular habitats (Snorrason et al., 1994), to acquire resources (Brönmark and Miner, 1992), to tolerate local conditions, to avoid predation (Brönmark and Miner, 1992), and especially to swim efficiently (Webb, 1984), many studies have looked at phenotypic variation in lake fishes and their consequences (Lindsay, 1981; Robinson et al., 1993; McLaughlin and Grant, 1994; Jastrebski and Robinson, 2004). The presence of two ecologically contrasting zones, the littoral and the pelagic, is often related to two specialized morphs faced with specific challenges associated to each of these environments. Pelagic fish need to swim long distances in order to search for patchily distributed resources, thus having greater swimming demands than littoral fish, which have access to more complex habitats, offering richer food resources and greater protection (McLaughlin and Grant, 1994; Bourke et al., 1997; Robinson and Parsons, 2002). These contrasting zones (*i.e.,* littoral *versus* pelagic) are often associated with distinct fish phenotypes in regards to body shape, fins insertion and, architecture of both mouth and gills. Some of the divergences and their anticipated advantages for each habitat were reviewed by Robinson and Parsons (2002) and are summarized in the table 3.1. Distinct morphotypes associated to pelagic and littoral zones were shown for many species such as: pumpkinseed sunfish *(Lepomis gibbosus)* (Robinson et al., 1993; Bhagat et al., 2006; Jastrebski and Robinson, 2004), bluegill sunfish *(Lepomis macrochirus)* (Robinson et al., 1993), lake whitefish *(Coregonus clupeaformis)* (Lindsay, 1981), three-spined stickleback *(Gasterosteus aculeatus)* (Schluter and McPhail, 1992; Schluter and Nagel, 1995) and Trinidadians guppies *(Poecilia reticulata)* (Robinson and Wilson, 1995). Different processes may drive differentiation patterns. Resources competition is considered one of the strongest forces to induce polymorphism and may lead to character displacement, which reduces competition after each morph specialized to a specific niche associated to different selective pressures (Gray and Robinson, 2002).

Table 3.1

Morphological features and expected functions of lake fish populations features inhabiting the littoral and pelagic zones, adapted from Robinson and Parsons (2002)

Morphological characteristics		Habitat		Expected advantage	
		Littoral	Pelagic	Littoral	Pelagic
Paired fins					
	Length and width	Larger	Smaller	Three dimensional maneuverability	Reduced drag
	Location	Lower	Higher		
Body form					
	Shape	Robust	Slender	Burst swimming	Reduced drag
	Head	Larger	Smaller		
Caudal pedoncule					
	Dorsal-ventral	Deeper	Shallower	Burst swimming	Cruising
	Lateral cross section	Compressed	Widened	Burst swimming	Cruising
	Length	Shorter	Longer	Burst swimming	Cruising
Mouth orientation					
		Subterminal	Terminal	Substrate prey capture	Water column or surface prey capture
			Upturned		
Mouth and jaws architecture					
		Larger	Smaller	Processing bigger, harder prey	Processing smaller, softer prey
		Robust	Reduced		
Gills raker architecture					
	Numbers and length	Fewer	More	Reduced clogging by	Planktivory
		Shorter	Longer	sediments	
	Interraker gap	Larger	Smaller		

The presence of a predator can also trigger phenotypic variation. For instance, populations of crucian carp (*Carassius carassius*) have deeper bodies in the presence of pike (*Esox lucius*), which can act as a defense against predation, given that bigger prey are more difficult to handle (Brönmark and Miner, 1992). Stream also present potentially contrasting mesohabitats (*e.g.,* riffle, run and pool), though much fewer studies have looked at phenotypic differentiation within these systems. One particular study shows that stream populations of pumpkinseed sunfish and rock bass *(Ambloplites rupestris)* have slender bodies, shallower but larger caudal peduncle and longer, more anterior inserted fins compared to lake populations (Brinsmead and Fox, 2002), suggesting that stream and pelagic morphologies converge. Furthermore, water velocity, which is highly variable in streams, has been linked to morphology and swimming capacity and it appears that fusiform fish are associated to faster current (McLaughlin and Grant, 1994; Peres-Neto and Magnan, 2004). Indeed, there should be a strong relationship between morphology and swimming capacity. For instance, a compact shape should enhance acceleration and maneuverability in complex habitats, while a fusiform shape should increase sustained swimming capacity allowing fish to cruise long distances at low costs (Webb, 1982; Taylor and McPhail, 1985). In addition, longer pectoral fins situated ventrally should increase maneuverability (Webb, 1984), but shorter fins should reduce drag (*i.e.,* force that oppose the motion of an object) (Drucker and Lauder, 2003). Stream fish may experience great temporal and spatial variation in their habitats, which may have important developmental consequences and/or act as a selective pressure in driving phenotypic variation. When relating trait variation to habitat variability within species, traits can vary in relation to mean, variance or both (fig. 3.1). Trait means should shift according to environmental gradients. It is anticipated that fish inhabiting fast flowing environments should have more fusiform bodies and a stronger sustained swimming capacity. Furthermore, heterogeneous habitats should favor greater trait variability and lower phenotypic integration (*i.e.,* correlations among traits) as an adaptation to cope with spatial environmental heterogeneity. Individual fish may require travelling across several mesohabitat units to achieve their daily and seasonal activities. Hence, at the population level, phenotypic variability could allow individuals to cope with the heterogeneous environment. We will assess whether contrasting stream mesohabitats (*e.g.,* riffle, run and pool) can lead to population differentiation regarding morphology and swimming capacity.

3.1.2 Evolution of phenotypic variability

Associations between environment and traits may result in the evolution of segregated and distinct individuals of the same species that live in sympatry but differ in habitat use, life-history, diet, morphology, physiology or behavior (Robinson and Wilson, 1994; Skúlason and Smith, 1995). Evolutionary theory suggests that constant and/or homogeneous environmental conditions should lead to a common phenotype and a lost of phenotypic variability. On the other hand, variable and/or heterogeneous conditions should favor phenotypic variability (Pigliucci et al., 2006). This trend has been demonstrated for plants (Schlichting, 1986; Pigliucci and Kolodynska, 2002; Pigliucci, 2005), fish (Brinsmead and Fox, 2002), amphibians (Van Buskirk, 2002) and was supported by theoretical models (Via and Lande, 1985; Scheiner, 1993; Scheiner, 1998; Sultan and Hamish 2002). According to Pigliucci (2005), phenotypic variability should confer better chances for populations to cope with variable environments. Phenotypic variation can be constrained by phenotypic integration which corresponds to the correlations among traits that can impose limits (*e.g.*, canalization) to traits to express variability (Peres-Neto and Magnan, 2004). Phenotypic integration can be quantified by calculating an integration index based on the variance of the eigenvalues from the partial warps representing morphological features. Phenotypic integration influences the potential for phenotypic variation, determining ecological and potentially evolutionary adjustments of the phenotype to the environment. Often, repeated patterns of phenotypic divergence across contrasting habitats and convergence across similar environments (*i.e.*, parallel evolution of independent populations) furnish strong evidence that local adaptations via selection is the most probable mechanism that lead to these patterns (Schluter and McPhail, 1993; Smith and Skúlason, 1996). In many cases polymorphism seems to be adaptive (Bourke et al., 1997). Indeed, littoral and pelagic morphs are more efficient in their habitat of origin (Robinson and Wilson, 1994; Skúlason and Smith, 1995), providing further evidence that evolution via natural selection has driven phenotypic divergence. This rationale can be applied to streams, in which riffles, runs and pools are different habitats regarding many characteristics that can impose divergent selective pressures and induce phenotypic variation (polymorphism) across these mesohabitat types.

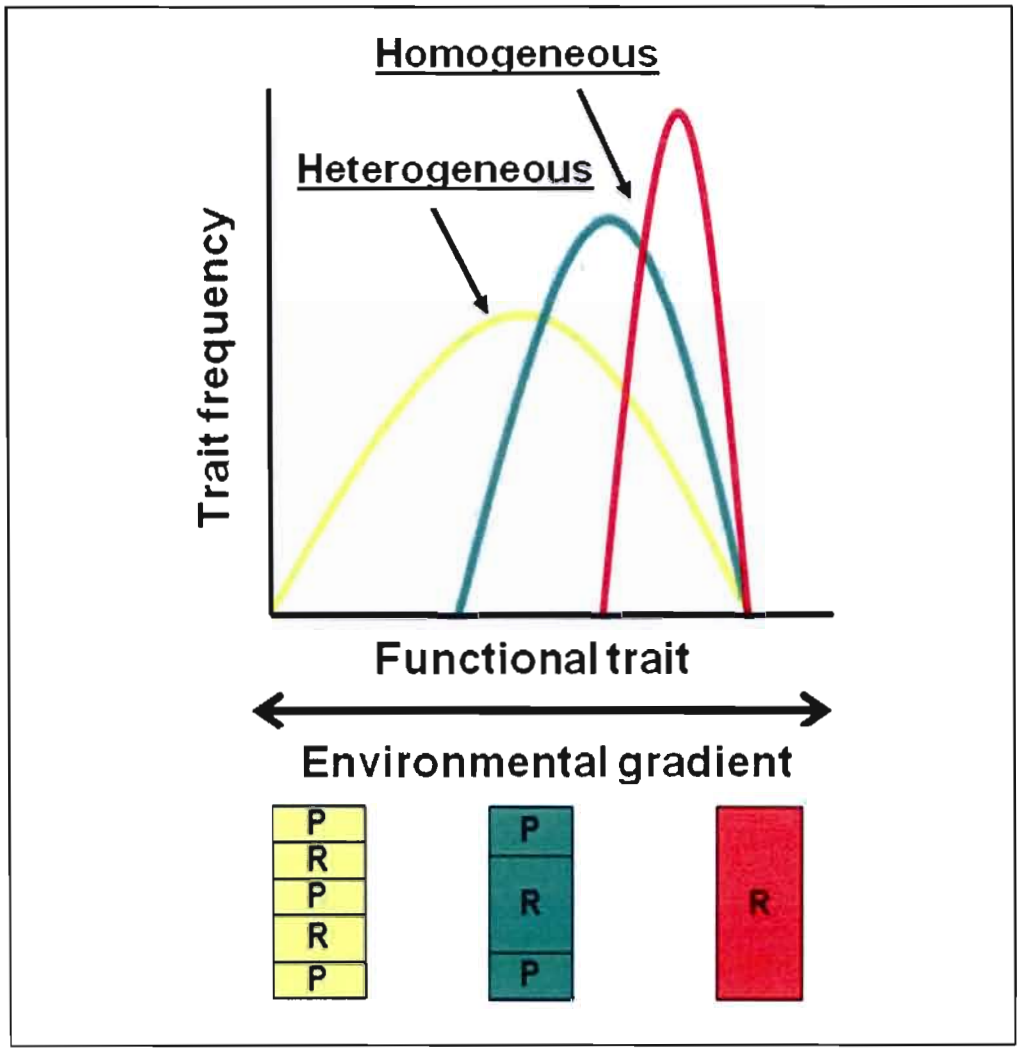


Figure 3.1 Conceptual illustration of the hypotheses concerning functional traits associated to sites encompassing different levels of habitat spatial composition shown at the bottom (R = Riffle, P = Pool). Mean and variance of functional traits can vary across populations inhabiting different environments. The means of functional traits should shift according to environmental gradients. For instance, as the proportion of riffle increases, the morphology could become more adapted to fast currents and fish should be more fusiform in order to increase sustained swimming capacity. Furthermore, heterogeneous environments could favor greater phenotypic variability. For instance, some habitats may be more heterogeneous and thus, traits could have greater variability. On the other hand, homogeneous sites, such as the red one composed only of riffles, could favor phenotypic integration and low trait variance.

The study of phenotypic variability within and across species may provide further insights about the processes that promote local adaptation at the population level and the factor that generate and maintain community structure, respectively.

3.1.3 Chapter objectives

If habitat selection, morphological characteristic and swimming capacity are linked, differences among riffles, runs and pools could parallel in some ways the ecological distinctions between littoral and pelagic zones of lakes. For instance, riffle fish, like pelagic fish, require greater sustained swimming capacity than pool or littoral fish, and must have distinct morphological features and swimming capacity. The specific objectives are as follows: (1) Assess and determine morphological variation within and between species across stream mesohabitat types and their relationship with environmental descriptors; (2) Quantify and compare phenotypic integration (*i.e.,* correlations among traits) within species across mesohabitat types and, (3) Estimate the relationship between habitat use, morphology and swimming capacity.

3.2 Methodology

A complete description of the study area, sampling design, environmental and fish sampling can be found in Chapter 1.

3.2.1 Fish morphology

Fish morphology was assessed by digital photography. Prior to digitalization, fish were anaesthetized with clove oil diluted in ethanol, ratio 1:10, to obtain a concentration of 40-50 mg eugenol/L of water (Anderson et al., 1997; Velisek et al., 2005). Once anaesthetized, fish were photographed on their left side on a ruler and then released where they were caught. Overall, more than 4000 fish belonging to 23 species were photographed. Since morphology is known to vary during fish development, we retained 1878 fish of similar size for a given species belonging to 10 species and 6 families distributed across stream mesohabitat (*i.e.*, riffle, run and pool) (tabl. 3.2).

Table 3.2

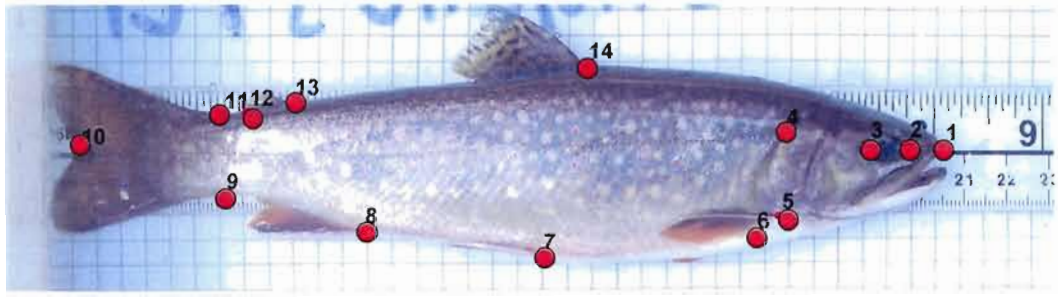
Species name, code, family and number of individuals by mesohabitat types retained for morphological analyses .

Species name	Species code	Family	Individuals by mesohabitat		
			Riffle	Run	Pool
Creek chub	SeAt	Cyprinidae	58	169	50
Pumpkinseed sunfish	LeGi	Centrarchidae	21	154	75
Rock bass	AmRu	Centrarchidae	62	114	41
Cut lips	ExMa	Cyprinidae	44	251	39
Brook trout	SaFo	Salmonidae	43	44	13
Central mudminnow	UmLi	Umbridae	3	213	121
White sucker	CaCo	Catostomidae	11	61	21
Yellow perch	PeFl	Percidae	11	68	27
Smallmouth bass	MiDo	Centrarchidae	25	29	5
Fallfish	SeCo	Cyprinidae	0	90	15

3.2.2 Geometric morphometrics

Geometric morphometrics was used to analyze fish morphology, a method based on comparing fish across homologous landmarks, (Marcus et al., 1996; Hjelm et al., 2001; Rüber and Adams, 2001). Geometric morphometrics uses the geometric positioning of landmarks in a Cartesian system. Compared to traditional morphological methods, geometric morphometrics are more effective at capturing information regarding the shape of an individual. With this method, relative position of features and fine morphological differences are possible to visualize, which makes it easier to compare morphological variation across different individuals and groups of individuals (Zelditch et al., 2004). Two-dimensional landmarks were positioned on digitized pictures with the program tpsDig2 (Rohlf, 2005a). Twelve homologous landmarks were used in order to characterize fish morphology, except for brook trout where we used fourteen landmarks to mark the insertion of the adipose fin (fig. 3.2). Then, generalized orthogonal least-squares Procrustes superimposition (GLS) was used to compare landmarks among groups. This analysis standardizes and rotates the coordinate (landmark) system to factor out fish size and minimize the sums of the squared distances between homologous landmarks; partial warps (a principal component analysis on the rotated configurations) were then produced and used as morphological variables (Zelditch et al., 2004). Partial warps are orthogonal to each other and can be used directly into statistical analyses to describe shape variation. Deformation grids allowed to visualize morphological variation among groups (*i.e.,* mesohabitats). The CoordGen6 program was used to conduct the Procrustes superimposition (Sheets, 2004a), PCAGen6 to calculate partial warps (Sheet, 2004b) and tpsRegr to visualize deformation grids according to predictor variables (Rohlf, 2005b).

a)



b)

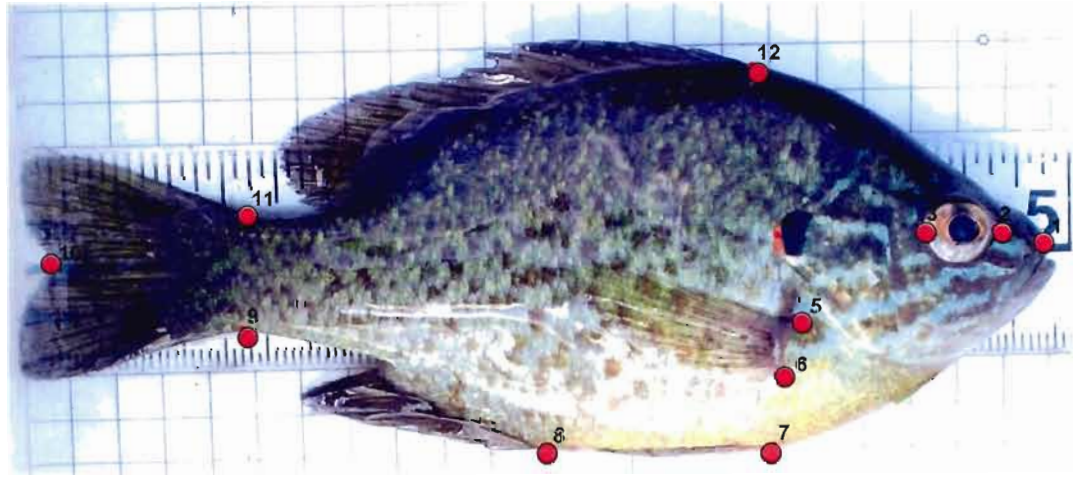


Figure 3.2 Illustration of the fourteen homologous landmarks used to describe brook trout morphology (a), and the twelve landmarks used for the nine other species (b).

3.2.3 Sustained swimming capacity

Fish were brought to the laboratory to evaluate their sustained swimming capacity. During the first 24 hours, they were acclimated and starved in oxygenated tanks at ambient temperatures (average tank temperature was 19.6 °C with a standard deviation of 1.3°C; average stream temperature was 20.4 °C with a standard deviation of 2.9°C). A standard sustained swimming protocol was used for each fish (Brett, 1964; Bell and Terhune, 1970; Kolok, 1999; Billman and Pyron, 2005) using a laminar flow flume (fig. 3.3). During the first 5 minutes after fish was placed in the flume, a constant small flow of 0.17 m/s was kept. Then, water velocity was increased gradually until fish reached exhaustion. Exhaustion was determined when fish stopped swimming and was pushed back against the chamber. Once the first signs of exhaustion were detected, a small 5V electric current was applied to compel swimming until complete exhaustion, in which case fish was not capable of swimming even under the application of the electric current. If exhaustion was not reached, the experience was terminated after 90 minutes at 0.57 m/s. After experimentation, fish was reintroduced in the tanks for another 24 hours and then returned to their original stream site and mesohabitat. The numbers of fish per species and mesohabitat types used in this experiment are indicated in table 3.3.

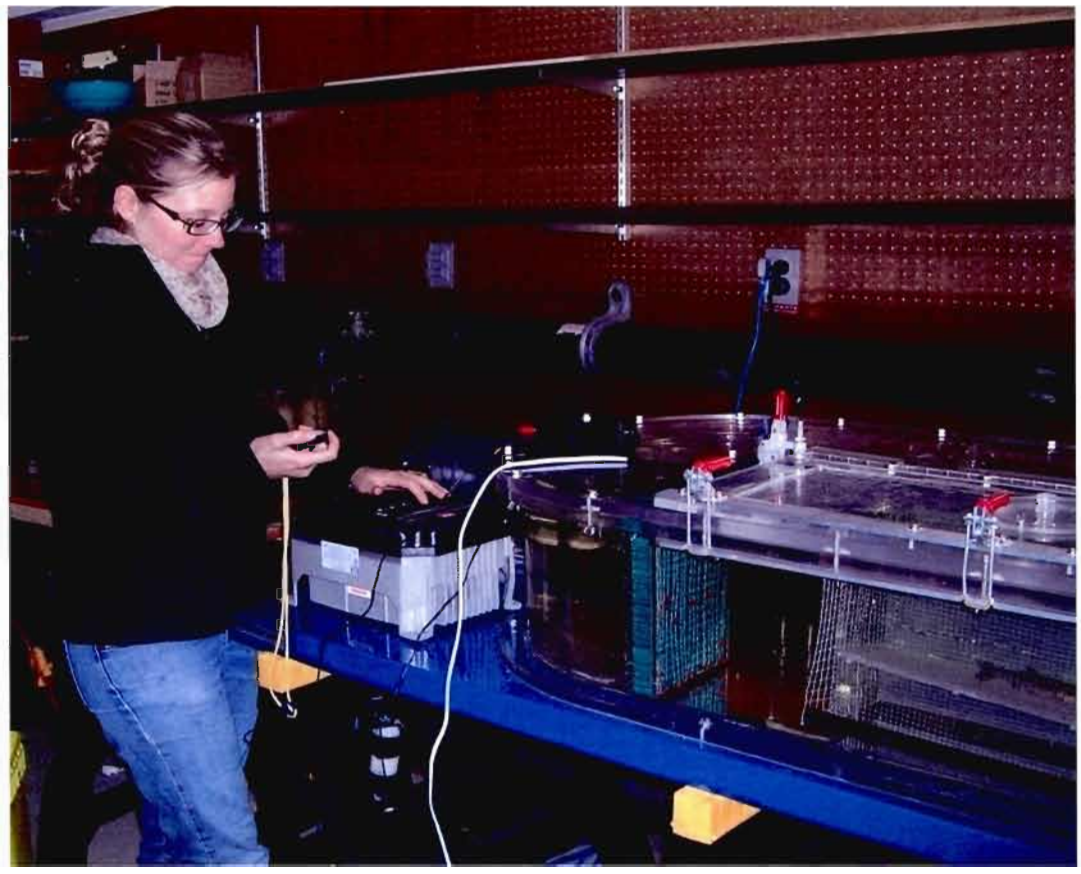


Figure 3.3 Illustration of the laminar flow flume used to assess fish sustained swimming capacity at the laboratory.

Table 3.3

Species names, code and number of individuals tested per mesohabitat for evaluating sustained swimming capacity

Species name	Species code	Individuals by mesohabitat		
		Riffle	Run	Pool
Creek chub	SeAt	5	12	8
Pumpkinseed sunfish	LeGi	0	31	36
Rock bass	AmRu	12	54	26
Cut lips	ExMa	12	42	12
Brook trout	SaFo	22	8	7
Central mudminnow	UmLi	0	4	8
White sucker	CaCo	2	12	2
Yellow perch	PeFl	3	5	8
Smallmouth bass	MiDo	16	4	4
Fallfish	SeCo	0	2	9

3.2.4 Statistical analyses

3.2.4.1 Among species morphological variations

A discriminant canonical analysis based on the partial warps was used to assess and visualize morphological differences and similarities among species. The discriminant analysis is a linear method which tests for differences in variables among species. The discriminant scores of each individual were recorded and used in further analyses. To facilitate interpretation of the results, we indicated throughout the methods section where the results of particular techniques are presented. The relative position of the ten species in the reduced multivariate space represented by the two first discriminant functions is shown in figure 3.4.

3.2.4.2 Within-species morphological variation across mesohabitats

We wanted to search for within-species morphological variation across mesohabitats. The number of individuals analyzed per mesohabitat was not similar across watersheds, which could induce a bias if there is a strong population differentiation at the watershed level, since they may represent large geographic landscape units with little genetic flow across them. The differences between morphology and mesohabitat types were tested with a MANOVA by permuting the partial warps within watersheds to control for this potential bias (tabl. 3.4). This analysis was conducted for each species in Matlab and 999 permutations were performed. In the case of significant morphological differences across habitat types, a discriminant analysis on species partial warps was conducted to assess variation across mesohabitats and pairwise post-hoc tests were used to contrast mesohabitats (tabl. 3.5). Deformation grids were produced to visualize within-species morphological variation across mesohabitats. The program tpsReg was used to produce deformation grids associated to mesohabitats by regressing the morphological partial warps, obtained from the original morphological coordinates, against the scores of the discriminant analyses obtained from the analyses presented in table 3.5.

3.2.4.3 Linking morphological variation to environmental variation

Since environmental variables bring specific information regarding mesohabitats, their relationship with morphological variation was also assessed. Individual discriminant function scores represented morphology and maximized differences across species (obtained from the 2 first axes of the analysis presented in figure 3.4) and their relationship with environmental variables was evaluated. A selection of the environmental variables was computed (function forward.sel written by Dray in the R software) for every species to identify which environmental descriptors were significantly linked to the morphological scores. Results are presented in table 3.6.

3.2.4.4 Comparison of phenotypic integration within species across mesohabitats

In order to estimate trait variation within species across mesohabitats, phenotypic integration was estimated from the partial warps by calculating an integration index based on the variance of the eigenvalues from the partial warps (Herrera et al., 2002; Peres-Neto and Magnan, 2004). When traits are highly correlated (*i.e.*, high phenotypic integration), the variance of the eigenvalues are greater than when traits (partials warps) are uncorrelated. Then, the level of phenotypic integration was compared within species across mesohabitats using the bootstrap procedures described in Peres-Neto and Magnan (2004; tabl. 3.7). These analyses were conducted in Matlab using 999 bootstrap resamples.

3.2.4.5 Linking sustained swimming capacity with species occurrence, habitat selection and morphology

In order to assess if swimming capacity was linked to patterns of species distribution and habitat preferences, the relationship between species sustained swimming capacity and the percentage of occurrence by sites and by sections, the percentage of used riffle, run and pool and the chi-square were assessed. These values were evaluated in the Chapter 1. Since morphological characteristics were expected to be linked to swimming capacity, this relationship was assessed by computing multiple regressions of species average partial warps

against average sustained swimming capacity. A factorial ANOVA was applied in order to evaluate the differences across species regarding their swimming capacity, mesohabitats and interaction (tabl. 3.8 and fig. 3.6). The analysis was conducted in Statistica software.

3.3 Results

The discriminant analysis was highly significant ($p = 0.0001$) where 99.89% of the individuals were correctly classified to according to their species (fig. 3.4). The first axis was mostly linked to general body form, streamlined species on the left side and fish with relatively deeper bodies on the right side, while the second axis discriminated species mostly according to head shape. A cluster according to family was apparent in figure 3.4. The centrarchidae (rock bass, pumpkinseed sunfish and smallmouth bass) and yellow perch were closely situated on the right side of the plot. The three minnows (creek chub, fallfish and cut lips) and brook trout were located near each other on the left side. The two benthic species (the central mudminnow and the white sucker) were both on the left side. However, there were differences concerning the second discriminant function, where, for instance, the central mudminnow was located on top and the white sucker on the bottom of the plot.

Morphological variation across mesohabitats was significant while controlling for the watersheds for eight out of the ten species (tabl. 3.4). For the two benthic species, the central mudminnow and the white sucker, it appeared that morphological differentiation was associated to differences across watersheds instead of habitat differences.

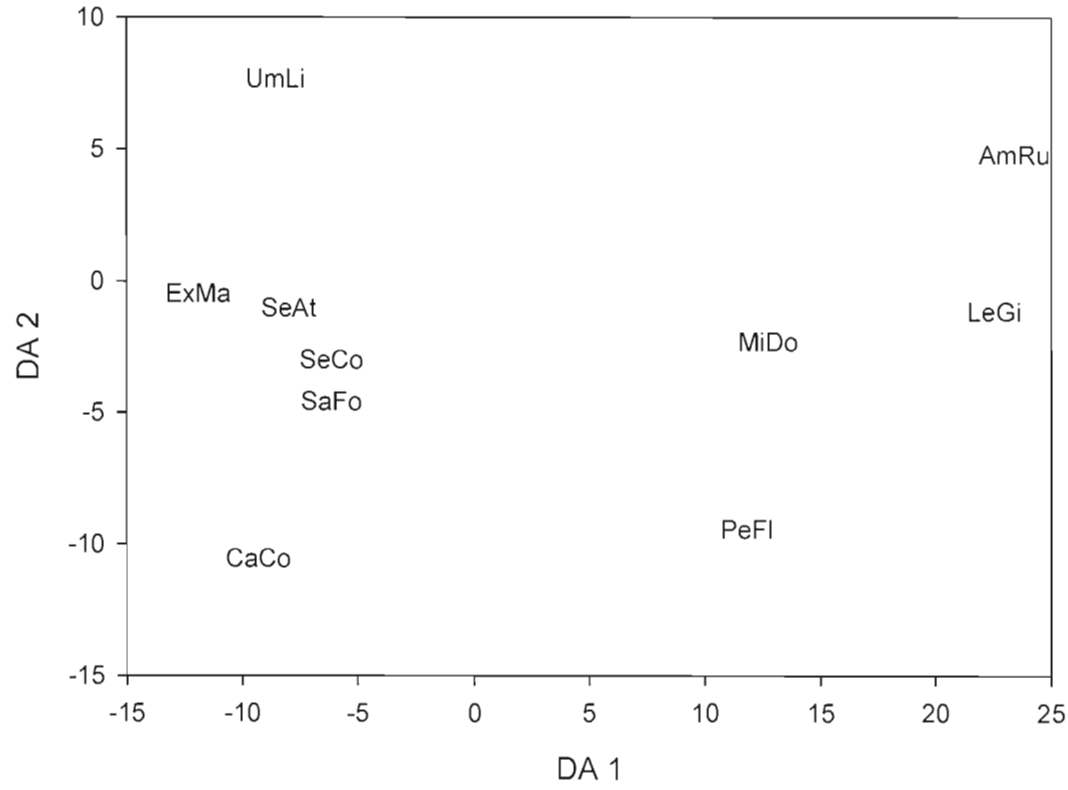


Figure 3.4 Species relative positions according to the two first discriminant functions computed on their respective partial warps.

Table 3.4

Result of the MANOVA for each species, partial warps were randomized within watershed to control for a potential spatial effect, species code, observed F statistic and probability are shown and, significant probabilities are in bold

Species code	Observed F statistic	Prob
SeAt	2.06	**0.0010**
LeGi	2.02	**0.0330**
AmRu	2.67	**0.0010**
ExMa	4.97	**0.0010**
SaFo	2.31	**0.0020**
UmLi	1.59	0.0961
CaCo	1.71	0.0841
PeFl	1.90	**0.0100**
MiDo	2.63	**0.0010**
SeCo	2.46	**0.0030**

Only the morphologies associated to the pairs of mesohabitats that were significantly different (tabl. 3.5) after controlling for watershed differences (tabl. 3.4) are presented in figure 3.5.Within species, on average, 79.5% of the individuals were correctly classified according to morphology to their own mesohabitat (tabl. 3.5). Results of the post-hoc tests indicate where the significant differences between pairs of mesohabitats lie, where two mesohabitats that are not connected by a line indicates that they are significantly different (tabl. 3.5). For instance, in the case of creek chub and yellow perch, the run habitat morphology was significantly different from the riffle and pool morphologies, whereas the latter two were similar. Pumpkinseed sunfish found in riffles had different morphology from those found in runs and pools. In the case of brook trout and smallmouth bass, the riffle and run morphology were significantly different. Although significant morphological divergences across mesohabitats were observed for all species, patterns in habitat differences are not always consistent across species.

Table 3.5

Results of the overall and post-hoc discriminant analyses for the morphological analyses, species code, Wilks Lambda, F statistic and probability, percentage of correct classification, post-hoc tests among mesohabitats are shown and, significant probabilities are in bold. The last species (SeCo) is found in only two mesohabitats (*e.g.*, run and pool)

Species code	Wilks' Lambda	F statistic	Prob	Percentage of classification	Post-hoc		
					Riffle	Run	Pool
SeAt	0.74	(40.51) = 2.06	**0.0002**	65	---		---

LeGi	0.72	(40.45) = 2.01	**0.0004**	69	---		
						---	---
AmRu	0.62	(40.39) = 2.67	**0**	66	---		

ExMa	0.58	(40.62) = 4.96	**0**	80	---		

SaFo	0.33	(48.14) = 2.30	**0.0001**	86	---		---
						---	---
PeFl	0.47	(40.16) = 1.89	**0.0027**	83	---		---

MiDo	0.17	(40.74) = 2.62	**0.0002**	92	---		---
						---	---
SeCo	0.63	(20.84) = 2.45	**0.0023**	95		---	

Only the morphology associated to the pairs of mesohabitats that were significantly different (tabl. 3.5) after controlling for the watershed (tabl. 3.4) were presented. For instance, in the case of creek chub, the run morphology was significantly different from the pool and riffle morphology, while these two morphs were similar. The riffle morphology presented a shorter body, a more upward mouth, larger eyes, and fins are inserted in a more anterior position compared to the run morphology. Pumpkinseed sunfish associated to riffles presented a deeper body, upward mouth, smaller eyes, more anterior dorsal and pectoral fins insertions, and more posterior anal and pelvic fins insertions than pool morphology. Rock bass were distinct across the three mesohabitats. Surprisingly, riffle and run morphologies were the most different, hence the pool morphology appeared intermediate. The riffle morphology had a longer body, upward mouth, larger eyes, more posterior anal and dorsal fins insertions and more anterior paired fins insertions, that pool but especially than run morphology. Cut lips were distinct across mesohabitats where riffles and pools were the most different. The riffle morphology had a slender body, smaller pectoral fin insertion and shorter caudal peduncle than the pool morphology. Brook trout associated to riffles had a bigger body, downward mouth, smaller eyes, more anterior pectoral fins and a shorter but higher caudal peduncle than the run morphology. Yellow perch coming from runs presented a slender body, downward mouth, bigger eyes, smaller and more posterior pectoral and pelvic fins insertions than yellow perch coming from pools. Smallmouth bass associated to riffles had a bigger body, more anterior pectoral fins and higher and longer caudal peduncle than run morphology. Fallfish coming from runs had a shorter body, upward mouth, bigger eye, more anterior pelvic and anal fins and, longer caudal peduncle than pool morphology. Overall, the deformation grids suggested no consistent patterns of morphological differentiation among species associated to their mesohabitats.

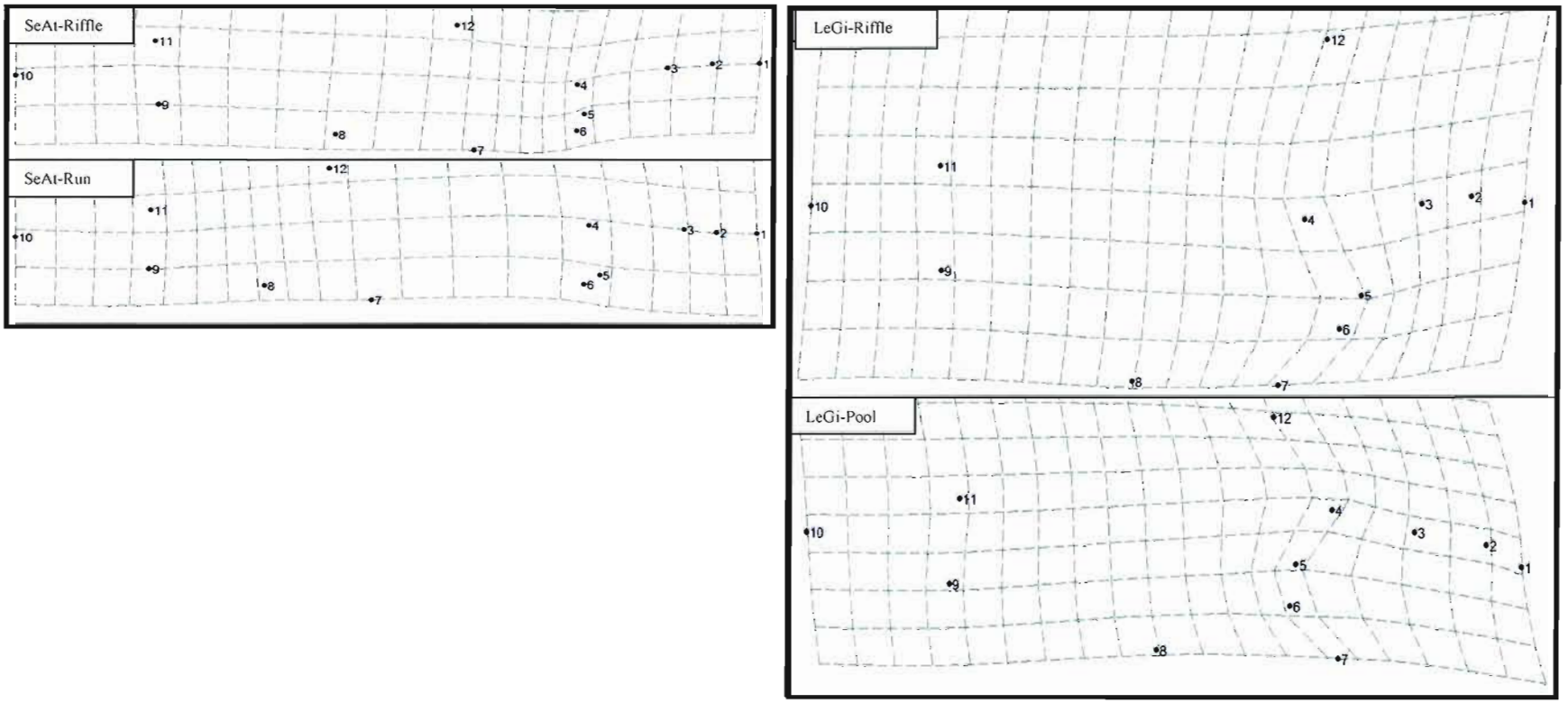


Figure 3.5 Deformation grids illustrating species significant morphological variation across mesohabitats. The amplitude of the divergences was magnified by a factor of 3.

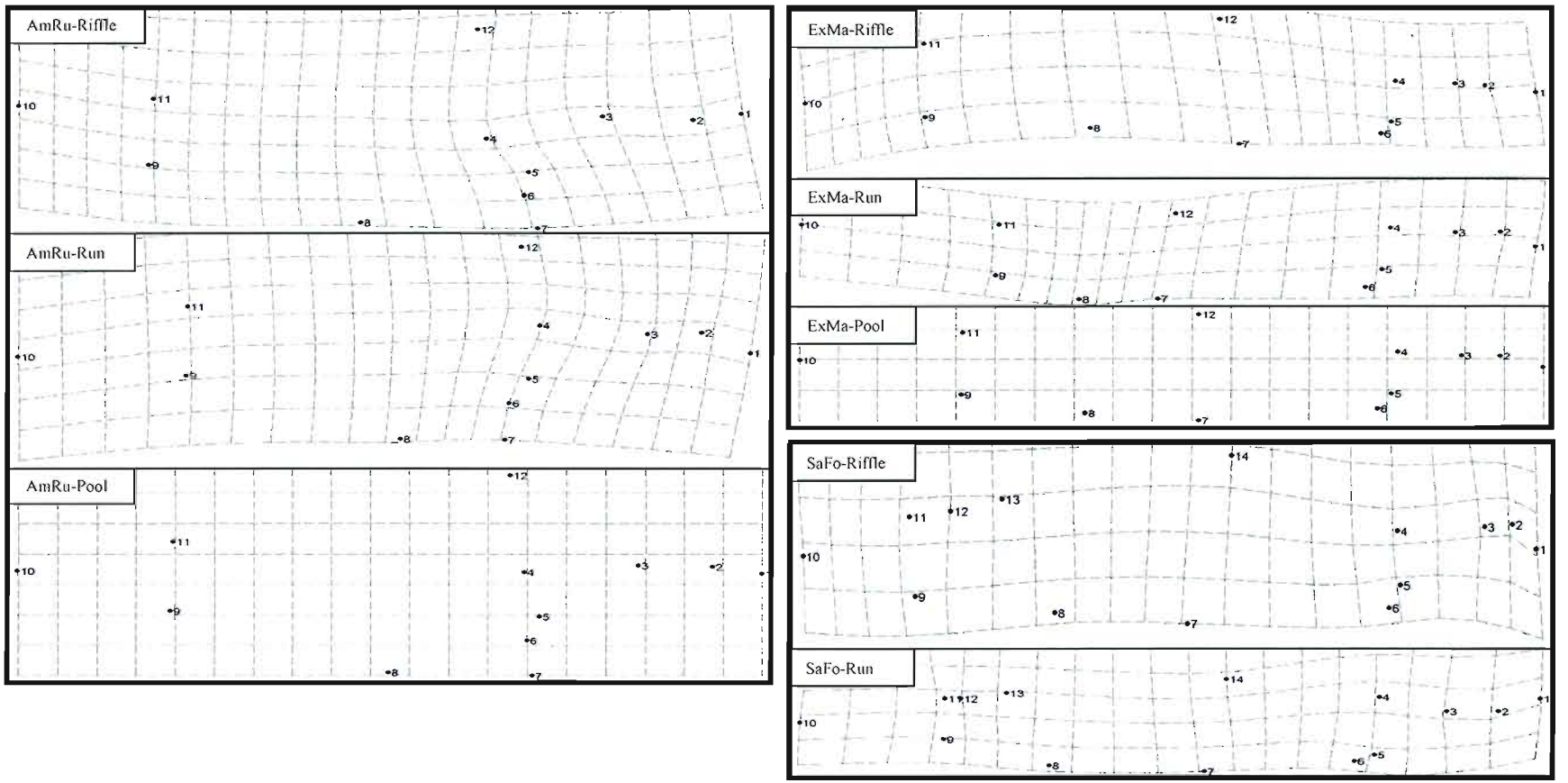


Figure 3.5 (continuation)

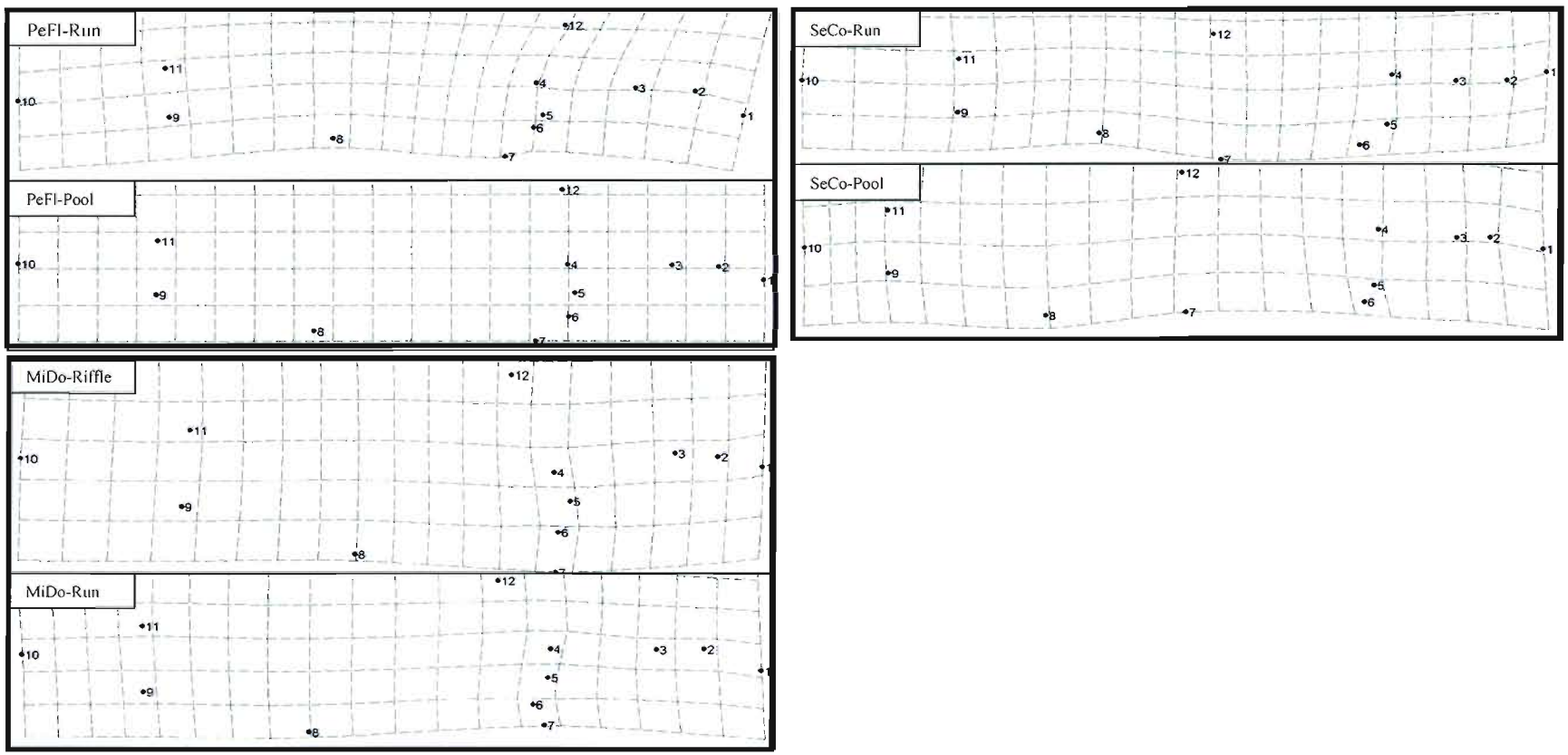


Figure 3.5 (continuation)

The forward selection detected significant relationship between morphology and environment for all species (tabl. 3.6). On average, 35% of the morphological variation across mesohabitats was explained by the environmental variables. This relationship varied from 20% for the central mudminnow to 58% for smallmouth bass. The variables that were most significant across species were: substrate type, temperature, bank and stream slope, width variation coefficient, average depth and flow.

The levels of phenotypic integration varied across species but the variations across mesohabitats for the ten species were not significant, except for the comparison between run and pool for the central mudminnow (tabl. 3.7). Thus, there was no much association between phenotypic integration and mesohabitats.

No significant correlation was found between species sustained swimming capacity and these values ($p > 0.15$ for all cases). The relationship between species morphology and sustained swimming capacity was assessed by computing multiple regressions of species average warps and average sustained swimming capacity. This relationship was also not significant ($p = 0.15$).

Table 3.6

Results of the forward selection of the environmental variables that were significantly linked to individual scores obtained from the discriminant analyses of the partials warps according to mesohabitats (fig. 3.4), species code, adjusted cumulated R2 (Adj. Cum R2), number of variables in the model, probability of the last variable entered are indicated and, significant probabilities are in bold

Species code	Adj.Cum.R2	Variable number	Prob
SeAt	0.21	10	**0.0230**
LeGi	0.30	13	**0.0490**
AmRu	0.30	9	**0.0120**
ExMa	0.25	6	**0.0050**
SaFo	0.47	6	**0.0050**
UmLi	0.20	7	**0.0440**
CaCo	0.44	9	**0.0470**
PeFl	0.29	4	**0.0270**
MiDo	0.58	7	**0.0100**
SeCo	0.48	9	**0.0340**

Table 3.7

Phenotypic integration index for each combination of mesohabitats, species code, eigenvalue variance and probabilitiy are indicated and, significant probabilities are in bold. The last species (SeCo) was found in only two mesohabitats (*e.g.*, run and pool)

	Variance			Probability of difference		
Species Code	Riffle	Run	Pool	Riffle/Run	Riffle/Pool	Run/Pool
SeAt	0.94	0.53	0.93	0.1902	0.8428	0.3323
LeGi	1.19	0.98	1.15	0.1782	0.0901	0.3664
AmRu	1.02	0.89	0.98	0.3964	0.5586	0.1461
ExMa	1.04	0.57	1.12	0.951	0.8529	0.7808
SaFo	1.32	1.06	3.02	0.6567	0.4685	0.8368
UmLi	10.64	0.71	0.68	0.8609	1.2272	**0.044**
CaCo	2.73	1.39	1.63	0.5966	0.7007	0.1321
PeFl	1.94	1.08	1.41	0.7528	0.5526	0.9149
MiDo	1.56	1.44	5.36	0.8268	0.8689	0.997
SeCo		0.91	1.89			0.8408

Differences across species and mesohabitats as well as their interaction on fish sustained swimming capacity were evaluated by a factorial ANOVA (tabl. 3.8). The main effects of species and mesohabitats as well as their interaction were all significant but only the interaction term is important here and its significance indicates that mesohabitat effect was not consistent across species (fig. 3.6).

Table 3.8

Results of the factorial ANOVA evaluating the effects of species identity and mesohabitat as well as their interaction on fish sustained swimming capacity, sum of square (SS), degrees of freedom (DF), mean square (MS), F statistic and associated probability are shown and, significant probabilities are in bold

	SS	DF	MS	F	Prob
Species	1.28E+04	6	2136	12.62	**0.0000**
Mesohabitat	712	1	712	4.21	**0.0410**
Species*Mesohabitat	4596	15	306	1.81	**0.0320**

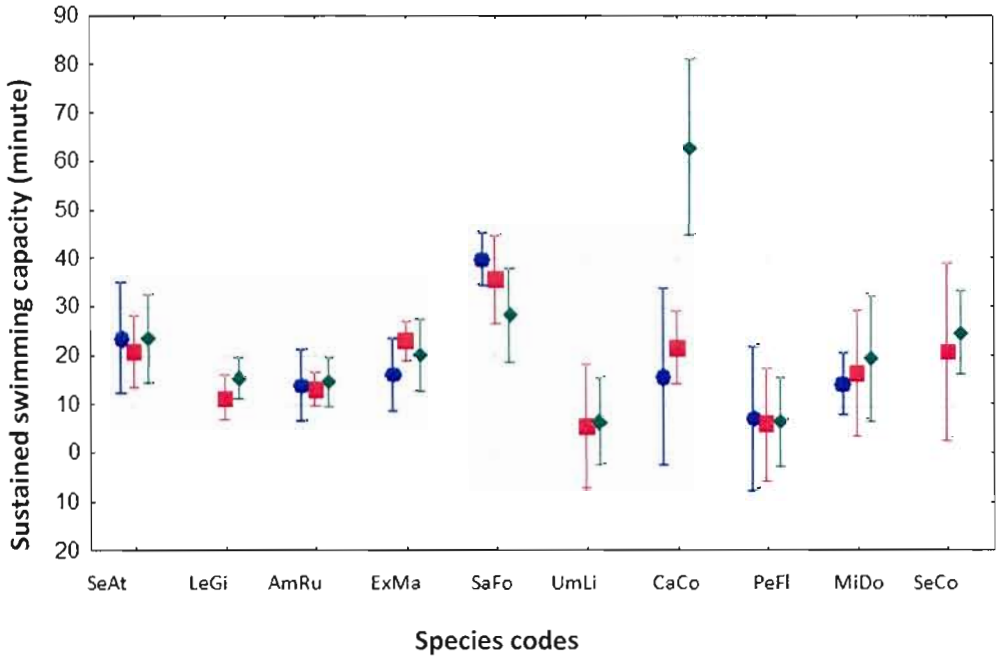


Figure 3.6 Interaction plots of species *versus* mesohabitats for the sustained swimming capacity. Species codes are indicated at the bottom and mesohabitats by symbols as follows: blue circles for riffles, red squares for runs, green diamonds for pools, and vertical bars denote 95% confidence intervals.

3.4 Discussion

One of the main goals of community ecology is to determine general patterns that allow understanding and forecasting ecological processes across time, space and taxonomic groups. One solution that has been proposed in order to improve the potential generality of ecological studies among taxonomic groups is to determine the importance of functional trait variation among and within species, and their functional relationships with environmental gradients (McIntyre et al., 1999; Lavorel and Garnier, 2002; Wright et al., 2005; McGill et al., 2006). In streams located in the Laurentian region, Québec, Canada, within and across species level of morphological and swimming capacity variability have been investigated and related to their mesohabitats and environmental characteristics. Although fish phenotypic differentiation has been reported (Bodaly, 1979; Baltz and Moyle, 1982), comparisons of local divergences (*e.g.,* mesohabitat) within different riverine species regarding morphology and swimming capacity as well as their functional relationships have not been yet explored.

3.4.1 Among species morphological variations

Highly significant morphological differences were observed among species and most variation was related to body shape. Morphological variation across species is larger than the one within species, suggesting that species may be an ecologically relevant unit to model. Moreover, morphological traits appeared related to species phylogeny, which is often used as a trait proxy (see Losos, 2008 for a review). Centrarchidae (*e.g.,* rock bass, smallmouth bass and pumpkinseed sunfish) and a percidae (*e.g.,* yellow perch) are close relatives and have a deeper body. Fish with a deeper body are known to suffer higher drag penalties when swimming and should be more adapted to complex maneuvering in slow environments (Webb, 1984), and indeed, those species are recognized to prefer low water flow (Bernatchez and Giroux, 2000). Cyprinidae (*e.g.,* creek chub, cut lips and fallfish), salmonidae (*e.g.,* brook trout), castostomidae (*e.g.,* white sucker) and umbridae (*e.g.,* central mudminnow) have a slender body. Such fusiform shape should reduce drag when swimming against the current (McLaughlin and Grant, 1994), allowing these species to swim in higher water flow. This trend is certainly true for brook trout (McLaughlin and Noakes, 1998; Bernatchez and

Giroux, 2000), but maybe less for the white sucker and the central mudminnow, which are known to be benthic (Bernatchez and Giroux, 2000). However, the fusiform shape of benthic species may help them to stay near the substrate without being dragged by water flow.

3.4.2 Within-species morphological variation across mesohabitats and environmental gradients

Morphological variation within species and across mesohabitats (*e.g.*, riffle, run and pool) was assessed in this study. Since divergent ecological strategies and morphological patterns across watersheds were reported in the literature (Bodaly, 1979; Baltz and Moyle, 1982), we evaluated morphological differences across mesohabitats while controlling for watersheds, and it remained significant for eight out of ten species. The environmental variables that best explained morphological variation within species were: substrate type, water temperature, bank and stream slope, width variation coefficient, average depth and flow. The two species that did not present significant phenotypic variation (*i.e.*, white sucker and central mudminnow) are benthic (Bernatchez and Giroux, 2000). At the bottom of the water column, velocity is minimal and may not be phenotypically selective (Hynes, 1970; Allan, 1995), which may explain why these species did not present much morphological differentiation across mesohabitats. Morphological features should be linked to environmental characteristics and habitat use. For instance, fusiform shape should reduce drag when swimming against the current and upward mouth should facilitate feeding at the surface of the water column (McLaughlin and Grant, 1994). A more anterior insertion of paired fins should improve fish ability to orient and maintain their position in the current and should assist with strong, steady swimming (Webb, 1984), larger eyes should provide a better visual acuity and a more robust caudal peduncle should accommodate a greater muscular mass (McLaughlin and Grant, 1994). For many species, population morphology associated to faster currents was more fusiform (*e.g.*, cut lips and yellow perch), mouth upwardly placed (*e.g.*, creek chub, fallfish, pumpkinseed sunfish and rock bass), fins were more anteriorly positioned (*e.g.*, creek chub, fallfish, pumpkinseed sunfish, rock bass, smallmouth bass and brook trout), eyes were larger (*e.g.*, creek chub, fallfish, rock bass and yellow perch) and caudal peduncle was bigger (*e.g.*, brook trout, smallmouth bass and fallfish). These

adaptations should allow fish to swim and feed efficiently in high flow. However, morphological differentiation across mesohabitats was different across species and patterns were not consistent across species within families either, indicating different challenges that are not associated to phylogenetic history.

Intraspecific variations were not conspicuous, but were detectable with the use of robust multivariate statistical methods. Nevertheless, subtle replicable differentiations are interesting as they may have consequences to fitness, foraging behaviour and swimming capacity (Robinson et al., 1993; Robinson and Wilson, 1994). Population differentiation may result from processes acting either at an ecological time scale (*i.e.,* plasticity) or on an evolutionary time scale (*i.e.,* drift or selection) (Pigliucci et al., 2006; Urban et al., 2008). For instance, both evolution and species sorting can drive trait value to produce a better match between the traits of resident individuals and local habitat conditions (Urban et al., 2008). Our study cannot assert whether the plasticity found is a function of the habitat or whether habitat choice is a function of the plasticity, or a combination of both. On the long term, similarities across populations should arise when they are exposed to analogous conditions in which similar traits are selected. However, at shorter periods, similar populations should seek for comparable habitat units where they are ecologically efficient and plasticity may quickly change trait expression as a way of tracking their environment. Note however, that evolutionary ecologists are only beginning to understand the conditions that favor either genetic differentiation or phenotypic plasticity within and across natural populations (Via and Lande, 1995; Schlichting, 1989; West-Eberhard, 1989). Even though this study was not designed to partition the plasticity and genetic components of the observed patterns, some issues may be still discussed in light of our results. They suggest that differentiation among populations can be observed over very small spatial scales (*e.g.,* mesohabitats) and across a wide range of species. If a strong genetic effect had driven the observed differences across mesohabitats, we would expect to find significant divergences among watersheds due to dispersal constrains and genetic flux among populations. The spatial structure of watersheds appeared to influence only benthic species. It is possible that they have lower dispersal capacities, promoting greater genetic differentiation and morphologies across watersheds.

Thus, for species having different ecotypes, our research suggests that selection may be the most likely mechanism responsible for some of the repeated (convergent) morphological divergences across mesohabitats. Those patterns of morphological variation should decrease intraspecific competition as phenotypic variability will increase adaptation to different habitats and facilitate the partitioning of resources and space (Gray and Robinson, 2002). Even though some species have preferential habitats, they are largely distributed throughout the studied landscape and across the considered habitats, and did not appear to compete (Chapter 1). Therefore, the relatively large levels of phenotypic variability observed may explain how these species are able to cope with high environmental variability and explore the heterogeneous environment encountered in stream systems. As stressed in Chapter 1, an important underlying assumption of modelling frameworks is that species are essentially the same entity throughout their range. In species that have the potential for physiological and morphological plasticity and local adaptation, this assumption may be invalid. Thus, when species occupy a wide range of environmental conditions these models become less efficient in determining the factors responsible for community structure. The findings of the present study indicate that some level of habitat specialization exists and vary across species, that environmental and habitat affinities are not extremely strong as show in Chapter 1 and the most likely explanation is that these species are capable of exploring these habitats due to their plasticity.

3.4.3 Comparison of phenotypic integration within species across mesohabitats

Phenotypic variation can be constrained by phenotypic integration which corresponds to the correlations among traits that can impose limits (*e.g.,* canalization) to traits to express variability (Peres-Neto and Magnan, 2004). High levels of phenotypic integration may impose restrictions on the range of trait that can be expressed and of environments that a species can inhabit (Schlichting, 1989). Characters having greater independence (*i.e.,* low phenotypic integration) should respond better to selection than highly associated traits (Lewontin, 1978). Constant and/or homogeneous environmental conditions should lead to a common phenotype, while variable and/or heterogeneous conditions should favor phenotypic variability (Pigliucci et al., 2006). In our case, phenotypic integration varied across species, suggesting higher trait plasticity and adaptive capacity for species displaying low phenotypic integration (*e.g.,* creek chub, pumpkinseed sunfish, rock bass and cut lips). However, contrarily to our expectations, no important difference was found within species across mesohabitats, except for the comparison between run and pool for the central mudminnow. Different populations of the same species appeared to have similar variance of trait expression and similar possibility to adapt to novel conditions throughout the landscape and mesohabitats. Intraspecific variation has been demonstrated experimentally, and water velocity appeared to decrease phenotypic integration for brook and Artic charr (*Salvelinus alpinus)* (Peres-Neto and Magnan, 2004). However, such difference has not been reported here; perhaps the number of individuals sampled was not large enough to identify this type of patterns or that mesohabitats were not sufficiently contrasted and isolated one from the other to trigger and maintain different level of phenotypic integration within species.

3.4.4 Linking sustained swimming capacity with species occurrence, habitat selection and morphology

The relationships between swimming capacity, species distribution, habitat selection and morphology have been investigated. Contrary to our expectations, no significant links were found between species sustained swimming capacity, morphological characteristics and distribution. A negative correlation between swimming capacity and habitat selection would

have suggested a trade-off between specialization, competitive ability and dispersal capacity. A positive correlation between swimming capacity and percentage of sites or sections occupied would have suggested a link between dispersal and geographic distribution range. Furthermore, fish sustained swimming capacity did not appear to be related to habitat type or morphology, even though some studies have observed patterns for those species (McLaughlin and Grant, 1994; McLaughlin and Noakes, 1998; Robinson and Parsons, 2002). Although differences encountered did not appear related to swimming, which is an important fitness aspect in fishes, we still need to explore how other aspects such as resource acquisition differ across mesohabitats. Another possibility is that our swimming experiments did not reflect the swimming challenges encountered by fish in the field. Indeed, in a stream, fish have other possibilities than facing the current, such as resting on the reach or keeping their position behind rock cracks to avoid high flow. These differential strategies could influence the difference in morphological patterns across species, thus explaining why patterns of morphological differentiation across mesohabitats were not consistent across species. For instance, it has been shown that the use of small scale current refuges reduce swimming costs in brook trout by 10% on average, while foraging ability was not affected (McLaughlin and Noakes, 1998). Thus, the use of such habitat structure provided individuals an energetic advantage. Many stream fish species undoubtedly use such refuges and backward areas to reduce swimming costs. It is likely that fish only utilize the faster flowing water when they have no other choice, such as feeding on invertebrate drifting in the current and this feeding may occur in sheltered locations whenever possible. The contrasts between our swimming experiment and riverine fish ecological activities may be responsible for the poor relationships observed with sustained swimming capacity.

3.4.3 Conclusion

Knowledge about phenotypic variability is important for diversity conservation and building appropriate distribution models. Species displaying important phenotypic variability should not be considered as a homogeneous unit with unique needs, but as a complex assemblage of distinct phenotypes. As human disturbances on ecosystems increase, phenotypic variability can allow individuals and also communities to cope with environmental variability, whereas species presenting low phenotypic variability may adapt less easily to environmental conditions. Our study adds to the growing body of evidence that suggests that contrasting habitat selection is an important mediator of evolution. Across mesohabitats, morphological features appeared to vary, but not the level of phenotypic integration and swimming capacity of riverine fish. Based on the results from this study, we suggest that to gain further insight on the mechanisms behind the development of polymorphism, the next step would be to disentangle the relative contribution of plasticity and genetics to phenotypic variation and integration. Moreover, another promising direction that should be considered is resource availability and consumption rates across habitat types. Indeed, apart from locomotion, species interactions such as direct resource competition may vary across habitats and may trigger character displacement, specialization and differentiation patterns. Finally, a swimming experiment that would match more closely the challenges encountered by fish could increase our understanding of the trade-offs among habitat use, morphology and swimming capacity.

CONCLUSION

Cette étude a été réalisée afin d'évaluer les relations entre les conditions environnementales et les traits fonctionnels pouvant influencer la structure des communautés de poissons de rivières à différentes échelles spatiales. Dans le premier chapitre, l'influence de l'environnement sur divers descripteurs biologiques évalués à 3 échelles spatiales (*e.g.*, bassin versant, site et section) a été déterminée pour 17 espèces de poissons de rivières. Dans le second chapitre, la relation entre l'environnement et la variabilité phénotypique de la morphologie et de la capacité de nage de 10 espèces de poissons des rivières a été évaluée. Pour ce faire, nous avons étudié les communautés de poissons de rivières dans la région des Laurentides au Québec, Canada. Le plan d'échantillonnage, inspiré par le réseau hydrographique de la région, était de nature hiérarchique. Il comprenait trois bassins versants (*e.g.*, rivière Rouge, du Nord et Ouareau), à l'intérieur desquels 39 sites ont été répartis et divisés en 143 sections au total, chacune associée à un type de mésohabitat (*e.g.*, rapide, droit et fosse). À l'échelle des sections, des conditions environnementales ont été évaluées afin de caractériser le milieu. Également pour chaque section, les poissons ont été capturés à la pêcheuse électrique, anesthésiés et photographiés afin de déterminer leur présence ou leur absence et leurs caractéristiques morphologiques en utilisant la géomorphométrie. De plus, certains poissons ont été rapportés au laboratoire afin de les soumettre à un protocole de nage standard pour évaluer leur capacité de nage soutenue.

Dans le premier chapitre, nous avons élaboré un cadre méthodologique afin d'identifier les échelles auxquelles différents processus structurent les communautés. Bien que la proportion de variance expliquée par les conditions environnementales à différentes échelles spatiales ait déjà été évaluée (Deschênes et Rodríguez, 2007; Reyjol et al., 2008), la comparaison de différentes espèces et de différents descripteurs biologiques était nécessaire. Ces contrastes peuvent identifier les échelles auxquelles un patron peut être détecté, en plus de recommander certaines conditions environnementales et grandeur de parcelle à échantillonner pour une espèce spécifique. À l'échelle des sections, 60% des espèces ont sélectionné des mésohabitats particuliers. Le courant élevé et turbulent présent dans les rapides (Hynes,

1970; Allan, 1995) semble limiter l'utilisation de cet habitat pour plusieurs espèces, particulièrement celles ayant un comportement benthique. Le partitionnement de la variabilité et de la relation entre l'environnement et la distribution des poissons, a suggéré que l'environnement, bien que variable principalement à petite échelle (*e.g.,* section) , semblait structurer les communautés à échelle intermédiaire (*e.g.,* site). L'absence de relation à petite échelle suggère que les poissons utilisent un espace plus grand qu'un mésohabitat afin d'accomplir leur activités quotidiennes telles se reposer, s'alimenter, se reproduire et éviter la prédation. À grande échelle (*e.g.,* bassin versant), il semble qu'il y ait peu de variation au niveau des conditions environnementales et de la composition des espèces. Des variations à grande échelle peuvent être présentes dans les communautés de rivières, mais à une échelle spatiale plus large que des bassins versants adjacents, par exemple entre différentes régions géographiques ou différents pays. Les patrons de cooccurrence ont semblé influencés par les conditions environnementales à toutes les échelles et par la structure spatiale principalement à grande échelle. Des interactions biotiques, indépendantes de l'environnement et de l'espace, ont été retrouvées à l'échelle des sites et des sections. Les espèces qui n'ont pas semblé affectées par les interactions biotiques sont caractérisées par un comportement généraliste et une diète variée. Les patrons de diversité hiérarchique ont suggéré que la communauté était variable à toutes les échelles, mais principalement à l'échelle des sites. L'influence de l'environnement et de la structure spatiale semble spécifique à l'échelle, l'espèce et le patron sélectionnés. Ce travail supporte la notion qu'il n'y a pas d'échelle idéale pour étudier les patrons biologiques et souligne la nécessité de considérer différentes échelles afin de comprendre l'assemblage des espèces en communautés. Des variations interspécifiques ont été observées et peuvent être expliquées par des traits fonctionnels, comme l'utilisation de l'habitat, la présence d'adaptation locale ou la capacité de nage et de dispersion. L'identification des échelles auxquelles les espèces répondent aux caractéristiques de l'environnement offre la possibilité aux gestionnaires d'appliquer les efforts de conservation au niveau approprié. Lorsque possible, des études préliminaires devraient être menées afin de déterminer l'échelle à laquelle les processus d'intérêt structurent les communautés avant de conduire un projet de grande envergure. Cette échelle adéquate de conservation dépend assurément aussi de certains traits fonctionnels des espèces. Par exemple, la gestion et la conservation de petites parcelles peuvent être utiles pour les espèces

dont la capacité de dispersion est faible, tandis que celles de grandes parcelles peuvent être nécessaires pour les espèces dont la capacité de dispersion est élevée.

Le second chapitre avait comme objectif d'évaluer la relation entre l'environnement et la variabilité phénotypique de la morphologie et de la capacité de nage des poissons de rivières. Les patrons de différentiation phénotypique permettent d'identifier des relations entre les caractéristiques des individus et les conditions environnementales, et des tendances généralisables entre les groupes taxonomiques (McIntyre et al., 1999; Lavorel et Garnier, 2002; McGill et al. 2007). Bien que des patrons de différentiation ont été reportés dans la littérature (Bodaly, 1979; Baltz et Moyle, 1982), la comparaison des divergences locales (*e.g.*, mésohabitat) concernant la morphologie et la capacité de nage de plusieurs espèces de poissons de rivières n'avait pas été réalisée. Des patrons de différentiation morphologique entre les mésohabitats étaient présents pour 80% des 10 espèces retenues. Ces variations morphologiques étaient présentes entre les populations provenant de différents mésohabitats indépendamment des bassins versants, mais n'étaient pas constantes entre les espèces. Si la génétique était principalement responsable des divergences morphologiques, on s'attendrait à retrouver des différences entre les bassins versants engendrées par des contraintes de dispersion et de flux génétique entre les populations. On a observé de telles différences seulement chez les espèces benthiques. Il est possible que ces dernières aient une plus faible capacité de dispersion, favorisant une différentiation génétique et phénotypique plus importante entre les bassins versants qu'entre les mésohabitats. De plus, une autre explication possible est que les espèces benthiques sont moins exposées et moins influencées par les variations des conditions environnementales, engendrant peu de différentiation phénotypique. Pour les espèces qui ont démontré des divergences, cette variabilité des traits morphologiques à petite échelle suggère un important niveau de plasticité phénotypique permettant aux individus de s'adapter rapidement aux conditions environnementales. Par contre, le mésohabitat n'a pas semblé affecter le niveau d'intégration phénotypique des populations, bien que des différences entre les espèces aient été retrouvées. Un faible niveau d'intégration phénotypique indique peu de corrélation entre les caractéristiques morphologiques, un potentiel élevé d'exprimer différentes combinaisons de traits et de s'adapter à de nouvelles

conditions. Ainsi, les populations d'une même espèce semblent avoir une capacité d'adaptation similaire à de nouvelles conditions environnementales. Des variations intraspécifiques ont été démontrées expérimentalement et un courant élevé semble diminuer l'intégration phénotypique (Peres-Neto et Magnan, 2004). Dans notre cas, il est possible que le nombre d'individus étudiés ait été insuffisant pour détecter de telles différences, ou bien que les mésohabitats ne sont pas suffisamment contrastés et isolés les uns des autres afin de générer et de maintenir différents niveaux d'intégration phénotypique au sein d'une même espèce. Aucune relation significative n'a été observée entre la capacité de nage et le type d'habitat, l'identité des espèces, les descripteurs reflétant la distribution ou la sélection d'habitat et la morphologie. Il est possible que les divergences morphologiques observées n'aient pas de lien fonctionnel avec la capacité de nage, mais plutôt avec d'autres aspects écologiques, comme l'acquisition des ressources ou les taux de consommation de différentes proies. Une autre possibilité est que l'expérience de nage n'ait pas reproduit fidèlement les défis écologiques auxquels sont confrontés les poissons. En effet, les poissons des rivières ont d'autres possibilités que de faire face au courant, telles suivre les berges ou les interstices entre les roches afin d'éviter les courants élevés (McLaughlin et Noakes, 1998). Ces différentes stratégies pourraient être spécifiques aux espèces et expliquer pourquoi les patrons de différentiation morphologique entre les types d'habitat ne sont pas consistants entre les espèces. Ce contraste entre l'expérience de nage et les activités quotidiennes des poissons pourrait être responsable du peu de relation significative observée.

Les différences morphologiques observées entre les populations suggèrent que les caractéristiques environnementales des mésohabitats puissent être un important médiateur de l'évolution chez les poissons de rivières. Par contre, cette variabilité phénotypique au sein d'une même espèce va à l'encontre d'une des prémisses de nombreuses études écologiques, soit qu'une espèce est la même entité dans l'ensemble du paysage étudié. Pour les espèces qui ont un fort potentiel de plasticité morphologique et physiologique ainsi que pour les adaptations locales, cette prémisse peut donc être invalide. Dans une perspective de gestion et de conservation, ces espèces polymorphiques ne devraient pas être considérées comme des entités homogènes, mais plutôt comme un assemblage complexe de phénotypes distincts, plus

ou moins flexibles. Dans ce cas, des modèles écologiques basés sur les populations plutôt que sur les espèces devraient améliorer la justesse des modèles et notre compréhension de la structure des communautés. Dans le système étudié, il est possible que l'importance des adaptations locales explique le peu d'influence qu'a l'environnement sur la distribution des poissons. En effet, à l'échelle des sections, l'environnement n'explique pas la distribution, mais la morphologie des poissons. Il semble que l'environnement induise des adaptations morphologiques locales qui permettent aux poissons de rivières de se distribuer dans l'ensemble des mésohabitats et des conditions environnementales de la région. Il est fort possible que l'environnement aurait eu un rôle plus important dans un modèle qui aurait ciblé les populations plutôt que les espèces. De futures études devraient quantifier l'information additionnelle apportée aux modèles écologiques décrivant différents patrons lorsque la variabilité phénotypique des populations est prise en considération.

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